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Scaling Up of Leaf Transpiration and Stomatal Conductance of *Eucalyptus grandis* x *Eucalyptus urophylla* in Response to Environmental Variables

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Additional information is available at the end of the chapter

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1. Introduction

Estimates of water use by plants are becoming increasingly important to forest science. Researchers apply water use estimates to predict the control of canopy conductance and transpiration [14, 26, 46], where this information is useful to help troubleshooting the water resources management [37, 24, 32], the role of transpiration in native forests [3] and to quantify the demand for water in short rotation forests and in plantations of *Eucalyptus* sp [10, 40, 41].

The growth and development of plants is a consequence of several physiological processes controlled by environmental conditions and genetic characteristics of each plant species. Therefore, in order to better understand the growth, development and hydrological impact of a *Eucalyptus* plantation, it is necessary to know the factors that control water use. Great efforts come up in order to investigate the contribution of water balance components in the productivity of eucalyptus, with the need to integrate the effects of climate and management practices on the production of wood from planted forests of *Eucalyptus*.

Process-based models consist in evidence-based relationships, which necessarily contain a relation of cause and effect, whether physical or biological [42]. A fundamental aspect of ecological processes is that they are affected by spatial and temporal dimensions. In spatial terms, for example, measurements made on a leaf in terms of net primary productivity, can not be extrapolated directly to the tree's canopy, because for this extrapolation is necessary knowledge about the distribution of the canopy, the arrangement of leaves, availability of soil water and others. Likewise, the extrapolation to the forest and the ecosystem needs information previously dispensable in smaller scales. This notion of scales and their

extrapolations are essential to avoid mistaken views and phenomena in a certain scale for larger or smaller scales. As the scale is broaden, more interactions occur between the growing number of compartments of the system, making it more difficult and laborious to study the cause-effect relationships from models based on processes.

Thus, this study aims to describe the ecophysiological behavior of *Eucalyptus grandis* x *Eucalyptus urophylla* at the leaf level in association with environmental variables in three stages of development, in order to provide subsidies for the development of models that can predict the ecophysiological responses of a lower scale and its extrapolation to a larger scale.

2. Determining the scales

For a description and quantification on the water flow of *Eucalyptus grandis* x *Eucalyptus urophylla*, in order to integrate information on the leaf scale from lower scales to a larger scale, the study was conducted in three different ages (scales) of different plant development, known as: pot, plot and watershed. For each scale, the seedlings of *Eucalyptus grandis* x *Eucalyptus urophylla* were produced by the method of mini-cuttings in plastic tubes in the clonal nursery. Within approximately 120 days, when they reached the conditions for dispatch to the field, were destined for planting in:

Pot Scale: The seedlings were transported to the experimental field of School Agricultural Engineering, University of Campinas - FEAGRI / UNICAMP and transplanted to pots of 100 dm³ (Figure 1a). These pots had circular holes in their sides and bottom, in order to allow better root aeration and drainage of excess water. The substrate was composed of vermiculite, coconut fiber and rice hulls. The ecophysiological study began 120 days after pot planting and measurements of transpiration, stomatal conductance, leaf water potential, photosynthetic active radiation and atmospheric vapor pressure deficit were carried out from February 2007 to June 2008.

Plot Scale: The seedlings were transferred to the experimental area of FEAGRI/UNICAMP and planted at 3 x 2 m spacing forming a clonal population. The predominant soil of the experimental area is classified as typical dystroferric Hapludox [9]. The ecophysiological study began at 240 days after planting (Figure 1b) and to assist data acquisition it was necessary to implant a measurement tower of 3 meters in height disposed between the crop rows to reach the treetops. The ecophysiological monitoring of transpiration, stomatal conductance, leaf water potential, photosynthetic active radiation and atmospheric vapor pressure deficit was conducted from January to July 2008.

Watershed Scale: The study was conducted at Santa Marta Farm, located in the Igaratá, São Paulo State. The geomorphological division of the State of Sao Paulo, according to the Institute for Technological Research [16], the study area is located in the Atlantic plateau that is characterized as a highland region, consisting predominantly of Precambrian crystalline rocks, cut by basic intrusive and alkaline Mesozoic-Tertiary rocks. The relief of

the watershed is called a relief of hills, dominated local amplitude 100-300 m and slopes of medium to high - above 15%, with high drainage density, closed to open valleys and alluvial plains inland restricted [16]. The soil of the plot of interest is the type Tb dystrophic Cambisol, Oxisols with clay. For monitoring the ecophysiological behavior, measurements were carried out in a stand of *Eucalyptus grandis* x *Eucalyptus urophylla*, 60 months after planting in 3 x 2 m spacing with the aid of a platform lift with a range of 18 meters in height (Figure 1c). Monitoring ecophysiological transpiration, stomatal conductance, leaf water potential, photosynthetic active radiation and vapor pressure deficit atmospheric were held throughout the month of August 2008.

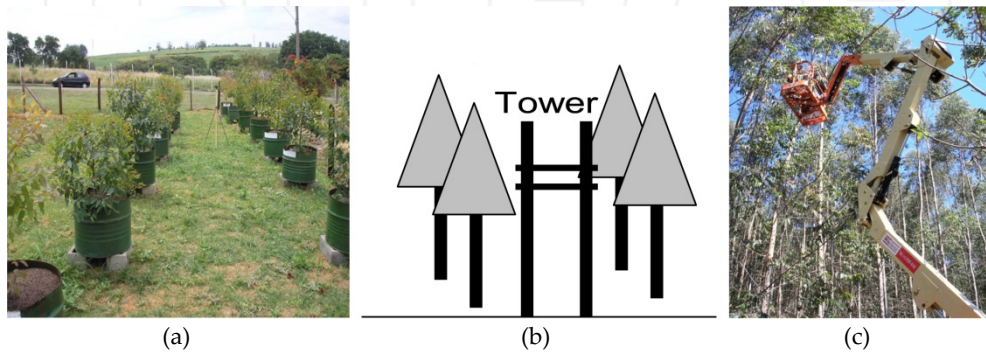


Figure 1. Scales: (a) Pot scale, (b) Plot scale and (c) Watershed scale: lift platform for observation of the variables used in ecophysiological clonal plantations of Santa Marta Farm, Igaratá-SP, Brazil.

2.1. Ecophysiological variables

The observations of water availability in the soil were performed by measuring predawn leaf water potential (Ψ_{pd}) using a Scholander pressure chamber [38], model 3035 (Soil Moisture Equipment Corp., USA) before sunrise in healthy leaves fully expanded. According to [45], Ψ_{pd} maintains a balanced relationship with the substrate's water potential, due to low rates of transpiration by plants presented overnight. To do so, four branches per seedling (on pot scale) or tree (on plot and watershed scales) were collected simultaneously. The measurements were carried out immediately after material collection.

Physiological measurements of transpiration (E) and stomatal conductance (Gs) were made by infrared gas analyzer (IRGA) LC-PRO + (ADC bioscientific Ltda., UK). For this end, four randomly and fully expanded healthy leaves for each individual seedlings/tree were chosen. The readings were held at hourly intervals throughout the day in the period from 8:00 am to 5:00 pm.

2.2. Environmental variables

Environmental variables such as photosynthetically active radiation and vapor pressure deficit of the atmosphere were chosen to correlate with the E and Gs. The PAR on the leaf

surface (Q_{leaf}) was determined simultaneously with measurements of ecophysiological variables, using the sensor coupled to the chamber of porometers, always disposed perpendicularly to incident sunlight on the leaf surface throughout each workday.

Additional data on air temperature and relative air humidity of the specific measurement days were obtained from an automatic weather station Campbell Scientific Inc. installed at the study site for each rating scale. This information was used to calculate the vapor pressure deficit of the atmosphere (VPD), as follows [30]:

$$VPD = es - ea, \text{ kPa} \quad (1)$$

The saturation of vapor pressure (es) was calculated using the following equation:

$$es = 0.6108 * 10^{7.5 * Tar / 237.3 + Tar}, \text{ kPa} \quad (2)$$

Tar = air temperature, °C

The partial vapor pressure (ea) was obtained by the following equation:

$$ea = RH * es / 100, \text{ kPa} \quad (3)$$

RH = relative humidity of the place, %.

2.3. Ecophysiological models and Scaling up

Structuring the ecophysiological model in the pot scale

The scaling up of information measured on the pot scale was performed by applying the ecophysiological model used by [45] in order to simulate the E and G_s according to Q_{leaf} , VPD and Ψ_{pd} considering the hourly time scale of the period of study. Thus, follows the equation:

$$E = f(\Psi_{pd}, Q_{leaf}, VPD) \quad (4)$$

$$G_s = f(\Psi_{pd}, Q_{leaf}, VPD) \quad (5)$$

The models that relate the E and G_s (dependent variables) and environmental variables Q_{leaf} VPD (independent variables) will be:

$$E = \beta_1 * Q_{leaf}^2 + \beta_1' * Q_{leaf} \quad (6)$$

$$G_s = \beta_2 * Q_{leaf}^2 + \beta_2' * Q_{leaf} \quad (7)$$

$$E = \beta_3 * VPD^2 + \beta_3' * VPD \quad (8)$$

$$G_s = \beta_4 * \ln VPD + \beta_4' \quad (9)$$

Where: E - leaf transpiration ($\text{mmol m}^{-2} \text{s}^{-1}$); G_s - leaf stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$); Q_{leaf} - photosynthetic active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$), VPD - vapor pressure deficit of the atmosphere (kPa), $\beta_1, \beta_2, \beta_3, \beta_4$ e $\beta_1', \beta_2', \beta_3', \beta_4'$ = coefficients to be explained for each scale and model.

Ecophysiological model calibration from pot to plot

The adjustment of the ecophysiological model developed at the pot scale was given by the angular coefficient k , obtained by the ratio between the equations generated for the pot and plot scale, thus being:

- E : Scaling up from pot to plot (E_p')

$$k = E_p / E_v \quad (10)$$

$$E_p' = E_p * k \quad (11)$$

Where: E_v - equation $E = f(Q_{\text{leaf}} \text{ or } VPD)$ on the pot scale; E_p - equation $E = f(Q_{\text{leaf}} \text{ or } VPD)$ to plot scale; E_p' - adjusted equation of scaling up of $E = f(Q_{\text{leaf}} \text{ or } VPD)$ from pot to plot by the angular coefficient of the model (k) to be specified for each scaling up.

- G_s : Scaling up from pot to plot (G_{sp}')

$$k = G_{sp} / G_{sv} \quad (12)$$

$$G_{sp}' = G_{sp} * k \quad (13)$$

Where: G_{sv} - equation $G_s = f(Q_{\text{leaf}} \text{ or } VPD)$ on the pot scale, G_{sp} - equation $G_s = f(Q_{\text{leaf}} \text{ or } VPD)$ to plot scale; G_{sp}' - adjusted equation of scaling up of $G_s = f(Q_{\text{leaf}} \text{ or } VPD)$ from pot to plot by the angular coefficient of the model (k) to be specified for each scaling up.

The same methodology was adopted for the adjustment of the pot scale model to watershed scale (E_B' and G_{sb}'') and plot to watershed (E_B'' and G_{sb}'''), being E_B - equation $E = f(Q_{\text{leaf}} \text{ or } VPD)$ and G_{sb} - equation $G_s = f(Q_{\text{leaf}} \text{ or } VPD)$ for watershed scale.

The ecophysiological model between the evaluation scales were subjected to analysis of variance and when significant, the means were compared by Tukey test using Minitab 14.0 software.

3. Case study: scaling up of the ecophysiological behavior of *Eucalyptus grandis* x *Eucalyptus urophylla* experience

Table 1 shows the daily mean of Ψ_{pd} and environmental variables. The highest water comfort occurred on the plot scale, where we also observed a higher mean rate of transpiration. In assessing the environmental variables, note that the VPD situation between

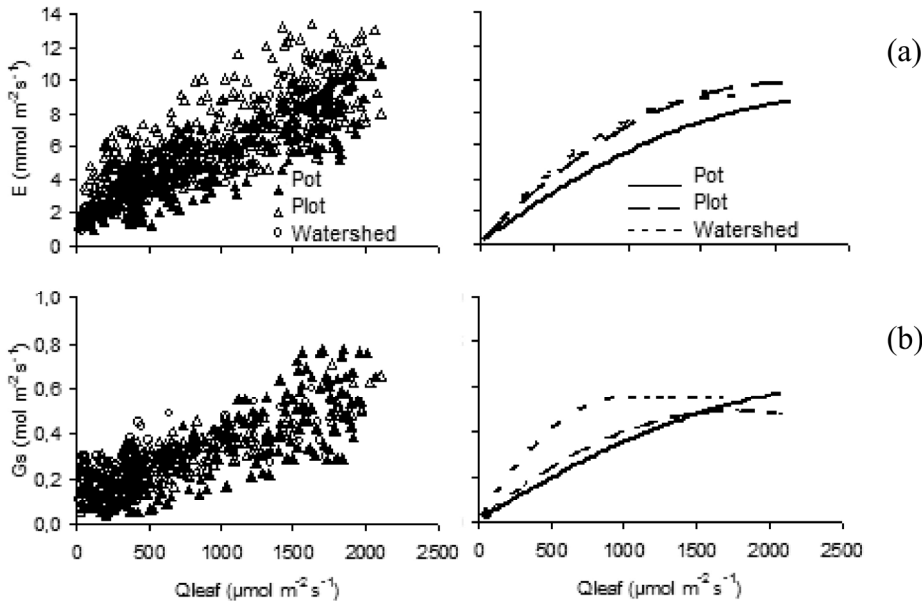
pot and plot, on average were similar, differing from the watershed scale that had mean lower than 33%, approximately. The energy available for physiological activity was higher in the pot scale, 100% higher than the watershed scale.

Variable	Pot	Plot	Watershed
Ψ_{pd} (MPa)	-0,30	-0,15	-0,21
VPD (kPa)	1,32	1,36	0,88
Q_{leaf} ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	1027	802	505

Table 1. Mean Ψ_{pd} and environmental variables for *Eucalyptus grandis* x *Eucalyptus urophylla* in the three scales.

3.1. Relation between E and Gs according to Q_{leaf} and VPD

Figure 2 shows the interactions between gas exchange and environmental variables Q_{leaf} and VPD. The values of E followed the evolution of Q_{leaf} and VPD being almost imperceptible the difference between the curves of the plot and watershed scale. The observed values for the pot and watershed scales were between 0.9 and 11.4 $\text{mol m}^{-2}\text{s}^{-1}$ and for the plot scale, 1.3 to 13.3 $\text{mol m}^{-2}\text{s}^{-1}$. The Gs also accompanied the increase in Q_{leaf} , however, the greater tendency was found in the watershed scale. As for the VPD, the Gs showed smaller response amplitude in the plot and watershed scales, concentrated on the range of 0.1 to 0.5 $\text{mol m}^{-2}\text{s}^{-1}$. On the pot scale, it was observed the reduction of Gs with increasing VPD, with values close to 0.8 $\text{mol m}^{-2}\text{s}^{-1}$ in situations of 1.0 kPa to 0.02 $\text{mol m}^{-2}\text{s}^{-1}$ in extremes of VPD (3.0 kPa).



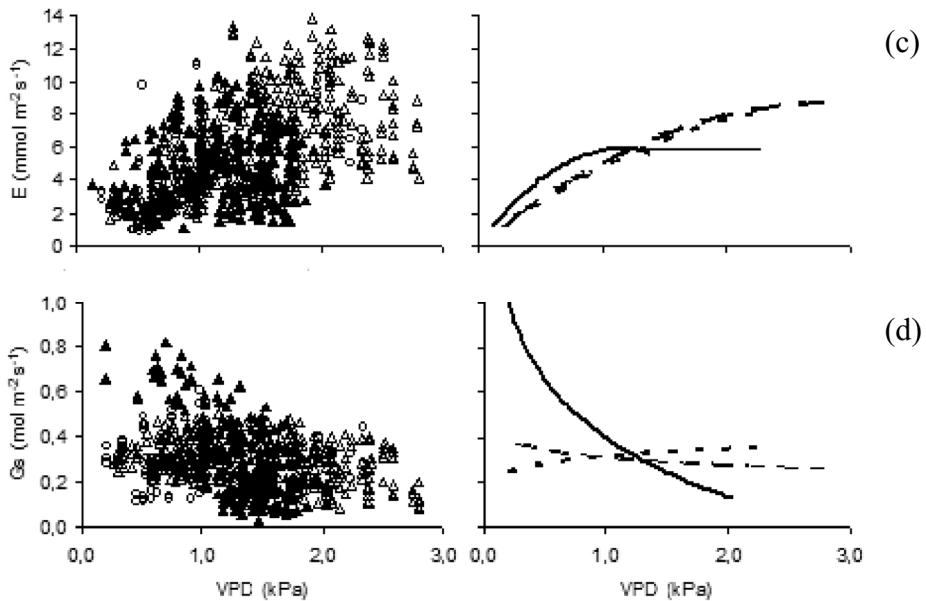


Figure 2. Behavior of $E \times Q_{leaf}$ (a), $G_s \times Q_{leaf}$ (b), $E \times VPD$ (c) and $G_s \times VPD$ (d) in the three scales of observation: pot, plot and watershed. Each point represents a mean of four measurements.

3.2. Interdependence of ecophysiological and environmental variables

In order to better understand the interdependence of ecophysiological variables (E and G_s) and environmental (Q_{leaf} and VPD), it was established a ratio between the hourly mean of all values observed during the study period, E , G_s and their respective hourly mean of Q_{leaf} and VPD (Table 2). With this mean ratio, we attempted to exclude the influence of variation of the concentration gradient of water and Q_{leaf} or VPD in order to characterize the difference in diffusion behavior according only to the structure and physiology of the *Eucalyptus grandis* x *Eucalyptus urophylla*. The differences between the scales of study were significant in almost all majority. The exceptions were observed in the E / VPD between the plot and watershed scales that were similar (Figure 2b) and the ratio G_s / VPD between the pot and watershed scales, in contrast in this case, to what it was observed in Figure 2d.

Between Scales	E/Q_{leaf}	E/VPD	G_s/Q_{leaf}	G_s/VPD
Pot x Plot	**	**	**	*
Pot x Watershed	**	**	**	ns
Plot x Watershed	**	ns	**	**

** e * = significant at 1% and 5% respectively, ns = non-significant

Table 2. Results of Tukey test comparing the means of the ratio E / Q_{leaf} , E / VPD , G_s / Q_{leaf} and G_s / VPD for *Eucalyptus grandis* x *Eucalyptus urophylla* in the three scales of study.

Table 3 presents the correlation matrix between ecophysiological and environmental variables in the three scales of study. The best associations were present in the relations E and Gs with Qleaf, reinforcing the behavior displayed in Figure 2. On the plot scale, all correlations presented were significant and as in the pot scale, the relation between Gs and VPD was found to be negative, while at the watershed scale it was not consistent.

Variables	Pot	Plot	Watershed
E x Qleaf	0,86**	0,83**	0,87*
E x VPD	0,30 ^{ns}	0,63**	0,56*
Gs x Qleaf	0,80**	0,85**	0,66*
Gs x VPD	-0,76**	-0,33**	0,07 ^{ns}

** e * = significant correlation at 1% and 5% respectively, ns = non-significant

Table 3. Simple correlation matrix between ecophysiological and environmental variables on pot, plot and watershed scales.

3.3. Scaling up: pot, plot and watershed

Analyses of variance among the parameters were significant at 1% probability. The mathematical equations as well as the comparison between the hourly mean values observed and simulated by the models are in Tables 4, 5, 6 and 7. Among the relations, E was associated more evenly with Qleaf, with the highest coefficients of determination (R^2) when compared to VPD, regardless of the scale of observation. For this reason, Qleaf can be used more safely than other variables for being more consistent.

In model $E = f(Qleaf)$ the mean test was significant for E_v and E_b' , indicating that the model of the pot scale, adjusted with k allowed extrapolation to the plot and watershed scales. Although the result of Table 2 has shown that the ratio $E/Qleaf$ between plot and watershed scales are statistically different, it was not necessary to use k for the prediction of E_b'' (Table 2). The values observed and simulated by the models were compared and showed good correlation coefficients (Figures 3a, 3b and 3c), although the model underestimated the values in some situations (Figures 3b and 3c). As for the variable G, the model $G_s = f(Qleaf)$ could be applied in scaling up G_{sp}' and G_{sb}' (Figure 4) not being significant for G_{sb}'' . The model $E = f(VPD)$ was adjusted for scaling up E_{vp} and E_{vb} , but in the extrapolation of plot scale to watershed scale it was not necessary to adjust the constant k, reinforcing what was already observed in Figure 2 and Table 2. Although in this case the scaling up being possible, the correlation coefficients between the observed and simulated values by the model were between 0.66 and 0.62 and were highly significant ($P < 0.01$) (Figures 3d, 3e and 3f). For $G_s = f(VPD)$, the proposed methodology can not be applied in any situation.

Scale	n	β_1	β_1'	R^2	$k \pm \text{S.D.}$	$E_m \pm \text{S.D.}$	$Q_{leafm} \pm \text{S.D.}$
Pot (E_v)	199	-0,000001	0,007	0,69	-	$5,41 \pm 2,07$ a	1027 ± 517
Plot (E_P)	516	-0,000002	0,0094	0,64	-	$5,60 \pm 2,27$ ab	802 ± 465
Watershed (E_B)	78	-0,000003	0,0106	0,83	-	$3,96 \pm 2,66$ c	505 ± 508
Scaling up (E_P')	516	-0,000001	0,007	1,00	$1,25 \pm 0,06$	$5,65 \pm 2,62$ b	802 ± 465
Scaling up (E_B')	78	-0,000001	0,007	1,00	$1,38 \pm 0,14$	$3,56 \pm 2,66$ c	505 ± 508
Scaling up (E_B'')	78	-0,000002	0,0094	1,00	-	$3,58 \pm 3,12$ c	505 ± 508

Means followed by same small letter in columns do not differ by Tukey test at 5% probability. n = number of measurements (mean of 4 measures).

Table 4. Model coefficients of $E = f(Q_{leaf})$ with observed data from E_v , E_P , E_B , and adjustment to simulate the scaling up (E_P' , E_B' , E_B''), coefficient of determination (R^2), k, E and Q_{leaf} mean \pm mean standard deviation (k and $E_m \pm \text{S.D.}$, $\text{mmol m}^{-2} \text{s}^{-1}$; $Q_{leafm} \pm \text{S.D.}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Scale	n	β_2	β_2'	R^2	$k \pm \text{S.D.}$	$G_{sm} \pm \text{S.D.}$	$Q_{leafm} \pm \text{S.D.}$
Pot (G_{sv})	199	-0,00000009	0,004	0,64	-	$0,34 \pm 0,16$ a	1027 ± 517
Plot (G_{sp})	516	-0,0000002	0,0006	0,59	-	$0,28 \pm 0,09$ b	802 ± 465
Watershed (G_{sb})	78	-0,0000005	0,0011	-0,17	-	$0,30 \pm 0,09$ bc	505 ± 508
Scaling up (G_{sp}')	516	-0,00000007	0,004	1,00	$1,31 \pm 0,12$	$0,26 \pm 0,10$ b	802 ± 465
Scaling up (G_{sb}')	78	-0,00000007	0,004	1,00	$2,26 \pm 0,53$	$0,26 \pm 0,19$ b	505 ± 508
Scaling up (G_{sb}'')	78	-0,0000002	0,0006	1,00	$1,43 \pm 0,41$	$0,18 \pm 0,11$ d	505 ± 508

Means followed by the same small letter in columns do not differ by Tukey test at 5% probability. n = number of measurements (mean of 4 measures).

Table 5. Model coefficients of $G_s = f(Q_{leaf})$ with observational data G_{sv} , G_{sp} , G_{sb} and adjustment to simulate scaling up (G_{sp}' , G_{sb}' , G_{sb}''), coefficient of determination (R^2), k, G_s and Q_{leaf} mean \pm mean standard deviation (k and $G_{sm} \pm \text{S.D.}$, $\text{mol m}^{-2} \text{s}^{-1}$; $Q_{leafm} \pm \text{S.D.}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Scale	n	β_3	β_3'	R^2	$k \pm \text{S.D.}$	$E_m \pm \text{S.D.}$	$VPD_m \pm \text{S.D.}$
Pot (E_v)	225	-0,4519	10,311	0,06	-	$5,07 \pm 1,87$ a	$1,23 \pm 0,35$
Plot (E_P)	506	-1,0627	6,0481	0,44	-	$5,75 \pm 2,32$ b	$1,33 \pm 0,49$
Watershed (E_B)	78	-0,927	5,6528	0,38	-	$3,96 \pm 2,62$ c	$0,88 \pm 0,41$
Scaling up (E_P')	506	-0,4519	10,311	1,00	$1,02 \pm 1,24$	$5,79 \pm 1,49$ b	$1,33 \pm 0,49$
Scaling up (E_B')	78	-0,4519	10,311	1,00	$0,57 \pm 1,26$	$3,99 \pm 1,47$ c	$0,88 \pm 0,41$
Scaling up (E_B'')	78	-1,0627	6,0481	1,00	-	$4,19 \pm 1,51$ c	$0,88 \pm 0,41$

Means followed by the same small letter in columns do not differ by Tukey test at 5% probability. n = number of measurements (mean of 4 measures).

Table 6. Model coefficients of $E = f(VPD)$ with observed data from E_v , E_P , E_B and adjustment to simulate scaling up (E_P' , E_B' , E_B''), coefficient of determination (R^2), k, E and VPD mean \pm mean standard deviation (k and $E_m \pm \text{S.D.}$, $\text{mmol m}^{-2} \text{s}^{-1}$; $VPD_m \pm \text{S.D.}$, kPa).

The scaling up with the involvement of the Q_{leaf} in E_B' and E_B'' generated values so similar that it is not possible to distinguish between these two models in Figures 3b and 3c. Similarly when using the variable VPD (Figure 3e, 3f).

Scale	n	β_4	β_4'	R^2	$k \pm \text{S.D.}$	$G_{sm} \pm \text{S.D.}$	$VPD_m \pm \text{S.D.}$
Pot (G_{sv})	225	-0,4015	0,4052	0,47	-	$0,33 \pm 0,19$ a	$1,32 \pm 0,30$
Plot (G_{sp})	506	-0,0505	0,3075	0,07	-	$0,30 \pm 0,08$ b	$1,36 \pm 0,51$
Watershed (G_{sb})	78	0,046	0,3092	0,52	-	$0,30 \pm 0,10$ b	$0,88 \pm 0,41$
Scaling up (G_{svp})	506	-0,4015	0,4052	1,00	$3,85 \pm 0,82$	$0,28 \pm 0,01$ c	$1,36 \pm 0,51$
Scaling up (G_{svb})	78	-0,4015	0,4052	1,00	$0,94 \pm 0,69$	$0,30 \pm 0,02$ d	$1,36 \pm 0,51$
Scaling up (G_{spb})	78	-0,0505	0,3075	1,00	$0,93 \pm 0,13$	$0,30 \pm 0,02$ e	$0,88 \pm 0,41$

Means followed by the same small letter in columns do not differ by Tukey test at 5% probability. n = number of measurements (mean of 4 measures).

Table 7. Model coefficients of $G_s = f(VPD)$ with observational data G_{sv} , G_{sp} , G_{sb} and adjustment to simulate scaling up (G_{sp}' , G_{sb}' , G_{sb}''), coefficient of determination (R^2), k, G_s and Q_{leaf} mean \pm mean standard deviation (k and $G_{sm} \pm \text{S.D.}$, $\text{mol m}^{-2} \text{s}^{-1}$; $VPD_m \pm \text{S.D.}$, kPa).

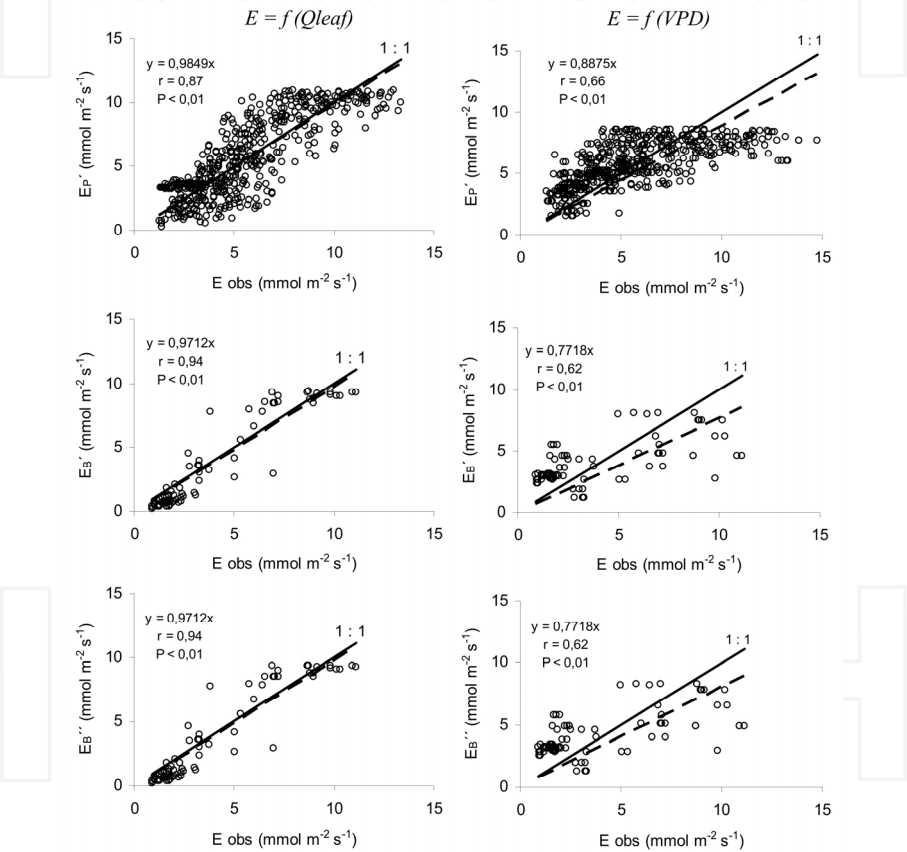


Figure 3. Linear regression (with intercept forced to zero) between the simulated values of E in the plot scale (E_p') from the observed data in the pot scale (E_{obs}) according to Q_{leaf} (a) and VPD (d), simulated values of E in the watershed scale (E_s') from the observed data on the pot scale (E_{obs}) according to Q_{leaf} (b) and VPD (e), simulated values of E in the watershed scale (E_b'') from the observed data in the plot scale (E_{obs}) according to Q_{leaf} (c) and VPD (f).

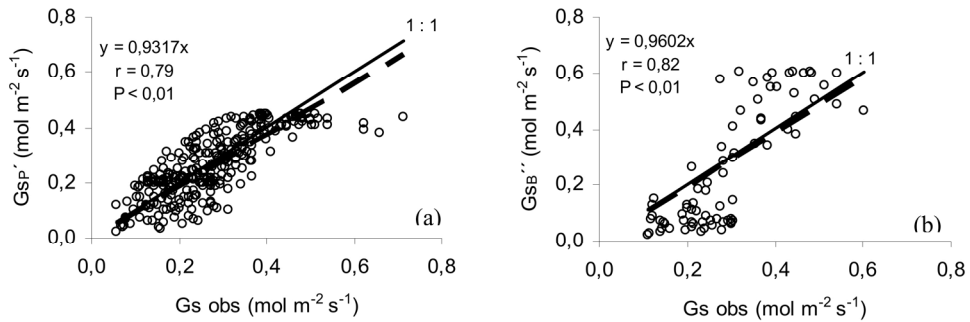


Figure 4. Linear regression (with intercept forced to zero) between the simulated values of Gs in the plot scale (G_{sp}') from the observed data on the pot scale ($G_s \text{ obs}$) (a), simulated values of Gs in watershed scale (G_{sb}'') from observed data on the pot scale ($G_s \text{ obs}$) (b) according to Qleaf.

4. Discussion

Many ecological studies are related to small spatial and temporal scales due to the easiness of operation and better understanding of the interaction of factors [18]. Considering this bias, the scaling up of information may constitute a useful tool for exploring upper scales from inferior ones and vice-versa [31]. This procedure involves a gradual process in which knowledge of how information is transferred from one scale to another is fundamental for understanding the mechanisms responsible for the natural generating of a standard phenomenon, which in turn are important for natural resource management. On the other hand, the scaling up is made from a reductionist perspective based on the detection mechanisms for determining the key processes operating at a certain level or scale, and its subsequent extrapolation to a higher or lower scale than the one studied [23].

From this principle, we could see the correlation between ecophysiological variables E and Gs with environmental variables Qleaf and VPD (Figure 2 and Table 3) in the three developmental stages of the *Eucalyptus grandis* x *Eucalyptus urophylla*. The characterization of the leaf behavior of E and Gs according to Qleaf and VPD from the pot scale to the watershed scale, we observed a similar tendency of response, which facilitated the extrapolation of the data from the pot scale to the plot/ or watershed scale in most relations, except for $G_s = f(VPD)$.

The behavior pattern of E and Gs according to Qleaf as observed in this study (Figure 2a, 2b, 2c), is well found in the literature [19, 22], as well as pattern of $G_s = f(VPD)$ for the pot scale (Figure 2d). However, the almost linear response pattern of $G_s = f(VPD)$ found in the plot and watershed scales showed lower Gs in these situations even with increasing VPD. This sharp difference in the tendency of response of $G_s = f(VPD)$ between the scale pot with the plot and watershed scales led to difficulty in adjusting the equations G_{sp} , G_{sb} and G_{spb} (Table 7).

According to [39] and [48] there are numerous observations that Gs decreases in response to an increase in VPD between the leaf and air. However, the plot and watershed scales, where

individuals were more mature than the pot scale, this behavior was somewhat modest, with little variation between the values of G_s . This fact can be justified by the findings obtained by [8] and [25], where they report that with the aging of individuals, the maximum levels of stomatal conductance decrease due to the greater sensitivity of stomata to the vapor pressure deficit of the atmosphere. Table 3 also shows the drop in correlation values between G_s and VPD with increasing age (scale) until appearing to be non-significant in the watershed scale.

In the other relations it was possible to predict the ecophysiological behavior with adjustment of the proposed model from young subjects, in this case, the pot scale with 120 days of age, for individuals with 240 days (plot scale) and for individuals with 60 months (watershed scale), approximately (Tables 4, 5 and 6). However, it also could be verified the accuracy of the model proposed for extrapolating the plot scale to the watershed scale in situations involving E , Q_{leaf} and VPD without adjusting the model (Tables 4 and 6). There is a clear similarity between the ecophysiological responses of these two scales in Figures 2a, 2b and 2c.

The use of models seeks to simplify the complexity of real world privileging certain fundamental aspects of a system at the expense of detail. To provide an approximate view of reality, a model must be simple enough to be understood and used, and complex enough to represent the system under study [1]. The idea of proposing a model based on environmental variables (Q_{leaf} and VPD) has been strengthened by [45], stating that the model reflects the conditions of the dynamics of the transport process in the soil-plant-atmosphere system, constituting the main component responsible for the flow of water in the plant.

Although the regression of E depending on Q_{leaf} and VPD (Figure 2a and 2c) show the proximity of the tendency of the response of E between the plot and watershed scales with increasing Q_{leaf} and / or VPD, the mean values obtained in field were lower for the watershed scale (Tables 4 and 6). This fact may be related to the reduced number of observations to the watershed scale compared to others, which may end up masking the results. Another important detail is related to environmental variables, both Q_{leaf} and VPD that present, on average, lower than in the days of assessment of the pot and plot scales.

In [20] throughout the work "Physiology in forest models: history and the future" discusses the importance of understanding the operation and its ecophysiological approach in models of forest production. In literature, several papers are presented in order to relate the highest rates of gas exchange and growth of individuals or young forests with more mature ones. In [5] for example, discuss that the forest productivity increases during the rotation, reaches a peak near the period when the leaf area is maximum and then decreases substantially. But the reasons for this decline are not yet completely understood [33, 47]. The latest hypothesis about the decline in productivity with age was developed by [34], called the hydraulic limitation hypothesis.

As trees age, their hydraulic properties change, and at the same time, the amount of radiation intercepted by the canopy varies substantially [17]. With the increased size of the

tree, water and nutrients must be transported over increasing distances between the root and the apex [7]. The water supply to the leaves of the apex becomes constrained by gravity and hydraulic conductance. These restrictions require a greater stomatal closure to maintain a minimum water potential to prevent xylem cavitation [15], resulting in decreases in gas exchange to a point where a positive carbon balance can not be achieved [4]. Some authors, by measuring transpiration by sap flow observed that the fall in productivity is accompanied by a decline in gas exchange rates [35, 2]. [28] studied the effects of age on the transpiration of a forest of *Pseudotsuga menziesii* of about 40 to 450 years of age in Oregon, USA, and by the sap flow methodology, also attributed to the hydraulic limitation hypothesis lower transpiration in individuals from the older forest, being that the highest transpiration of the 40 year-old forest provides further evidence of change in the local water balance because of its higher transpiration. In [2], on their turn, reported that the hydraulic limitation hypothesis proposes that the increased distance to be traveled by water inside the plant reduces the hydraulic conductance of the leaf. If the stoma closes to regulate the status of leaf water potential, taller trees will close their stomata at low vapor pressure deficits when compared to younger or shorter trees. Again, this report confirms the behavior observed in the plot and watershed scales to $G_s = f(VPD)$ (Fig. 2d, Table 3), however it was not the behavior observed for transpiration.

It is recognized that low pressure of water vapor between the leaf interior and the outside air (VPD) is an important environmental factor that affects the functioning of stomata. However, the causes for this event are still much discussed in the literature. The [44] examined the stomatal response to VPD in higher plants and the possible mechanisms proposed to explain this response. According to the author, the results are conflicting. When there is stomatal response to VPD, the mechanism that causes this response is also not well understood, being two hypotheses proposed for this mechanism. The hypothesis of "feedforward," which considers the decrease of G_s directly with increasing VPD, and abscisic acid (ABA), the signal for the response. In the event of feedback, G_s decreases with increasing VPD due to the increase in leaf transpiration, which lowers the water potential in the leaf. That is, the increase in E could be responsible for stomatal closure due to increased water potential gradient between guard cells and other epidermal cells or simply by reducing the leaf water potential [11, 27, 43]. These two mechanisms have been the subject of debate in the scientific community, for there are results published in the literature to support both hypotheses.

In any case, our results agree with the behavior explained by the hypothesis of feedback, even because we did not analyze the ABA during the study. [44] concludes his work as an unresolved issue, justifying the continuation of research in this area.

The hydraulic limitation hypothesis in some other studies failed to explain the reduced growth [2, 36] and the mechanism responsible for this fact was not identified. The [33] believes that there is no universal mechanism to explain the decline in productivity with increasing tree height, but that there are various components involved.

In searching for the characterization of the ecophysiological behavior of eucalyptus at different ages, [10] related to leaf area and rate of growth of *Eucalyptus globulus* Labill at the

age of 2-8 years with stomatal conductance and transpiration by the method of sap flow in Australia. These authors observed an increase in transpiration of the stand from 2 to 5 years of age, where it reached to the peak in rates of exchange with subsequent decline thereafter. This decrease was related to the decline of leaf area index, with the result in annual growth rates and efficiency of water use. Although in our study, transpiration and stomatal conductance have been obtained at leaf scale by porometry, these variables had the same behavior found by them, i.e., the major tendencies of transpiration rates were observed in the plot and watershed scales, where individuals were more developed. We should also remember that the measurements, at whatever age (pot, plot or watershed scales), were always performed only in fully expanded leaves at the top of the canopy directly exposed to solar radiation. The difference between our study and [10] is that the evaluations performed by the method of sap flow are closely related to the total leaf area of the crown, without the need to quantify the leaves that consist it, nor the diversity in the degree of development of each one of them. The leaf area index is generally considered the most important determinant of differences in transpiration between different forest stands [13, 28]. Generally, young forests have a higher concentration of leaf area in a single layer of canopy, while as the tree grows, the leaves are more uniformly distributed in generating various vertical profiles of leaf area [29] and these changes in the distribution of stem and leaves can have pervasive effects on canopy transpiration.

The justification of this work for having higher gas exchange tendencies, at the leaf level, in the plot and watershed scales may be explained by the fact that individuals did not reach their peak of development, as justified by [10]. Thus, the physiological activities continue to "full steam" favoring the growth of biomass. So that, in terms of forest production, in the decision making about the best time for cutting the planted forest (*Eucalyptus* sp), it is studied the balance of production curves and mean and yearly increments, with the aim of identifying the maximum mean rate of increase in production. When this point is reached, it is said that this is the peak production of the forest, that is, when it reaches its greatest efficiency in production (technical age for cut-off). After this peak, there is a decline in the production curve, and economically speaking it is not feasible to keep the tree standing.

The scaling up of information held on a lower scale to a higher scale is more problematic for several reasons. The transpiration of most plant species, including eucalyptus, is determined by several factors that vary continuously. In addition to age, among them are climatic demand (solar radiation and vapor pressure deficit of the atmosphere, temperature and wind speed), the physiological mechanisms related to the stomatal response to environmental factors, water availability and soil nutrients [6, 20]. Another issue addressed by [12] which is normal to expect that the rate of perspiration varies from species to species, as well as vegetative growth.

Since transpiration is related to the development of leaf area in plantations of short duration such as eucalyptus, which have high rates of initial growth, can also happen fast maximization of water use by these crops, which ultimately generate implications for the prediction of its water needs and impacts on watershed hydrology.

A fundamental aspect of ecological processes is that they are affected by spatial and temporal dimensions. In spatial terms, for example, measurements made on a leaf in terms of net primary productivity, can not be extrapolated directly to the tree, because for this extrapolation it is necessary knowledge about the distribution of the canopy, the arrangement of leaves, availability of soil water etc. Likewise, the extrapolation to the forest and the ecosystem needs information previously dispensable in smaller scales. This study focused on all measurements, only fully expanded leaves and fully disposed to incident radiation. In fact, we know that there is no way to expand these results to an already formed canopy, since in this case, the leaves do not have a uniform development, as well as variation in the incidence of radiation and, thus, there is a need for additional data that were not addressed in this study. However, tendencies were observed and simulated by the models developed. This notion of scales and their extrapolations are essential to avoid mistaken views and phenomena in a certain scale to larger or smaller scales. As a scale is broadened, most interactions occur between the growing number of compartments of the system, making it more difficult and laborious studies of cause-effect relationships from models based on processes.

Adding to the complexity of understanding the interactions between the ecophysiological variables, there is also the difficulty of the experimental protocol. This fact reinforces the merits of the methodology presented here. As stated by [21] in order to generate practical tools, such calculations based on processes must be combined with empirical relations derived from experiments and measurements carried out over several periods.

5. Conclusions

The relations between E and G_s with Q_{leaf} and VPD showed significant differences at 1 or 5% in all relations of scaling up, except for the relation $E \times VPD$ in scaling up of plot / watershed, and $G_s \times VPD$ pot / watershed. The relation that had the best response between E and G_s and environmental variables was E / Q_{leaf} whose correlation was significant on all scales at 1 or 5%. The measured values of E and G_s were consistently above the plot and watershed scales compared to the pot scale. For each lower scale, a model was developed for scaling up into a higher scale. It was possible to perform the scaling up (pot, plot and watershed scale) of E and G_s . The simulation models of E according to Q_{leaf} / VPD and G_s and Q_{leaf} / VPD proved robust in each of the scales. There was no need to adjust the models of scaling up between plot and watershed in relations involving E and Q_{leaf} , and E and VPD . All results were obtained for Ψ_{pd} between 0 to -0.5 MPa. It is suggested that measurements of E and G_s are carried out in three scales in others Ψ_{pd} to confirm the findings of this study.

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