

Forest biomass variation in Southernmost Brazil: the impact of Araucaria trees

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Received 04-III-2013. Corrected 07-X-2013. Accepted 11-XI-2013.

Abstract: A variety of environmental and biotic factors determine vegetation growth and affect plant biomass accumulation. From temperature to species composition, aboveground biomass storage in forest ecosystems is influenced by a number of variables and usually presents a high spatial variability. With this focus, the aim of the study was to evaluate the variables affecting live aboveground forest biomass (AGB) in Subtropical Moist Forests of Southern Brazil, and to analyze the spatial distribution of biomass estimates. Data from a forest inventory performed in the State of Rio Grande do Sul, Southern Brazil, was used in the present study. Thirty-eight 1-ha plots were sampled and all trees with DBH ≥ 9.5 cm were included for biomass estimation. Values for aboveground biomass were obtained using published allometric equations. Environmental and biotic variables (elevation, rainfall, temperature, soils, stem density and species diversity) were obtained from the literature or calculated from the dataset. For the total dataset, mean AGB was 195.2Mg/ha. Estimates differed between Broadleaf and Mixed Coniferous-Broadleaf forests: mean AGB was lower in Broadleaf Forests ($AGB_{BF}=118.9$ Mg/ha) when compared to Mixed Forests ($AGB_{MF}=250.3$ Mg/ha). There was a high spatial and local variability in our dataset, even within forest types. This condition is normal in tropical forests and is usually attributed to the presence of large trees. The explanatory multiple regressions were influenced mainly by elevation and explained 50.7% of the variation in AGB. Stem density, diversity and organic matter also influenced biomass variation. The results from our study showed a positive relationship between aboveground biomass and elevation. Therefore, higher values of AGB are located at higher elevations and subjected to cooler temperatures and wetter climate. There seems to be an important contribution of the coniferous species *Araucaria angustifolia* in Mixed Forest plots, as it presented significantly higher biomass than angiosperm species. In Brazil, this endangered species is part of a high diversity forest (Araucaria Forest) and has the potential for biomass storage. The results of the present study show the spatial and local variability in aboveground biomass in subtropical forests and highlight the importance of these ecosystems in global carbon stock, stimulating the improvement of future biomass estimates. Rev. Biol. Trop. 62 (1): 359-372. Epub 2014 March 01.

Key words: indirect methods, carbon stock, regression model, deciduous forests, spatial distribution.

Nutrients, water availability, seasonality, temperature and disturbance all influence plant biomass accumulation. At a regional scale vegetation growth and biomass build up are affected by soil moisture (Raich et al., 1991), mean annual temperature (Raich, Russel, Kitayama, Parton, & Vitousek, 2006), rainfall seasonality (Ter Steege et al., 2003; Saatchi, Houghton, Dos Santos Alvalá, Soares, & Yu,

2007), altitude (Tanner, Vitousek, & Cuevas, 1998; Alves et al., 2010) and soil characteristics (Laurance et al., 1999; DeWalt & Chave, 2004; Castilho et al., 2006). In tropical forests the trend is the reduction in productivity, height and growth of trees with increasing altitude (Tanner et al., 1998; but see Alves et al., 2010 for a different pattern in Southeast Brazil). Soil fertility and mean annual temperature are



positively related to productivity and biomass in these forests (Laurance et al., 1999; DeWalt & Chave, 2004; Raich et al., 2006; Larjavaara & Muller-Landau, 2012), as opposed to rainfall limitation (increasing number of dry months) that appear to reduce aboveground biomass and tree density (Ter Steege et al., 2003; Saatchi et al., 2007).

Biotic factors, such as species richness and diversity, may also be prominent in biomass build up. The increase in number of species (richness) of an experimental grassland community subjected to elevated levels of CO₂ may enhance local biomass storage (Tilman, Knops, Wedin, & Reich, 2002), due to the range of functional groups within the community (Reich et al., 2001). At broader spatial scales, species richness seems to influence the amount of carbon accumulated in terrestrial ecosystems (Catovsky, Bradford, & Hector, 2002). Bunker et al. (2005) suggested that carbon storage in tropical forests is also dependent on species composition, in agreement with the idea that high species diversity may increase carbon accumulation. It has been recently suggested that species richness and composition have impacts on biomass production (Cardinale et al., 2007) with a possible positive effect on aboveground biomass. Although there are a number of grassland studies relating biomass to species diversity (Tilman et al., 2002; Van Ruijven & Berendse, 2009; Hector et al., 2011), this pattern is not clear for forest ecosystems.

Aboveground biomass distribution usually shows high spatial variability (Clark & Clark, 2000; DeWalt & Chave, 2004). Species composition and stem size distribution influence aboveground biomass affecting local and regional variability (Souza, Cortez, & Longhi, 2012). Large trees have high biomass due to their diameter and height, although medium size trees, due to their abundance, contribute with an important proportion of the average biomass per plot (Keller, Palace, & Hurr, 2001). Site-to-site variation may be explained by the presence/absence of large trees (e.g. DBH greater than 60cm), since the basal area of those trees may explain up to 50% in the variation of AGB

among plots (Baker et al., 2004) and account for a large proportion of AGB (Brown, 2002). Regional variability of AGB, on the other hand, may be also influenced by the variation in species composition. This variation is usually accounted for in biomass estimates by the inclusion of wood density in allometric equations as it considers regional differences between forests with regard to species composition (Baker et al., 2004; Vieira et al., 2008). Natural disturbances and environmental changes also affect aboveground biomass, causing spatial variability: simple gap openings or complex effects like the El Niño-Southern Oscillation (ENSO) may increase mortality of large trees and cause spatial/temporal variability (Chave, Riéra, & Dubois, 2001; Rolim, Jesus, Nascimento, Couto, & Chambers, 2005). The removal of species with high wood density, large trunk diameter and high basal area may deplete carbon stock in forests up to 70% (Bunker et al., 2005).

Much of the attention given to the study of forest biomass emphasizes high diversity forests located in tropical regions of Asia, Africa and the Neotropics, especially in the Amazon. Temperate forests are also a focus of study and they are thought to be one of the most carbon dense forests in the world (Dixon et al., 1994; Keith, Mackey, & Lindenmayer, 2009). Subtropical forests have received fewer published results as compared to tropical forests (e.g., Gasparri, Grau, & Manghi, 2008). Subtropical ecoregions, however, may contain a significant proportion of terrestrial biomass due to the presence of conifers, especially in mixed conifer-broadleaf forests, since many conifers have slow growth and may accumulate high biomass (Brodribb, Pitterman, & Coomes, 2012). In addition, biomass estimates for poorly-sampled regions are needed to calibrate broad-scale biomass estimates based on satellite images (Baccini, Laporte, Goetz, Sun, & Dong, 2008; Goetz et al., 2009). In this sense, obtaining new estimates for unstudied areas and reducing uncertainty with respect to the spatial distribution of biomass estimates in subtropical forests would improve remote sensing data and global

biomass-carbon maps (Baccini et al., 2008; Saatchi et al., 2011).

We tested the validity of the following expectations: (1) Greater aboveground biomass estimates are located in areas where temperature is warm and rainfall is homogeneously distributed throughout the year, due to the dependency of biomass accumulation on temperature and rainfall (Ter Steege et al., 2003; Raich et al., 2006; Saatchi et al., 2007). (2) Aboveground biomass increases with density of adult trees ($DBH \geq 10\text{cm}$) (Clark & Clark, 2000; Souza et al., 2012) and species diversity, following the positive relationship between aboveground biomass and species diversity found in grassland studies (Tilman et al., 2002; Cardinale et al., 2007). (3) Forests containing conifer species (Mixed Conifer-Broadleaf Forests) should present higher biomass estimates when compared to Broadleaf Forests in the region (Lamloom & Savidge, 2003; Souza, 2007).

MATERIALS AND METHODS

Study plots: According to the Köppen-Geiger climate classification, the state of Rio Grande do Sul (Southern Brazil, average latitude 30°S and 53°W) is classified as Cfa, a temperate humid climate type, presenting a hot summer (temperature of the hottest month $>22^{\circ}\text{C}$) and lacking a true dry season (Peel, Finlayson, & McMahon, 2007). In the North (mainly the Northeast quarter), soils are derived from volcanic rocks and altitude presents a gradient of increasing elevation from West (ca. 200m.a.s.l.) to East (ca. 800m.a.s.l.; Ker, Almeida, Fasolo, & Hochmüller, 1986; Streck et al., 2008). The central region of the State is located in a depression, presenting lower elevation (from 40 to 100m) and soils derived from sedimentary rocks (Streck et al., 2008). Slopes are steeper in the Northeast and deep valleys dominate the edges of the plateau, while in the center, slopes are mild and a network of rivers is responsible for the drainage of the region (Streck et al., 2008).

Southern Brazilian forests are included in the Atlantic Forest global region and are classified as Subtropical Moist Forests, according to the Terrestrial Ecoregions proposed by Olson et al. (2001). The study region encompasses two major forests types: Broadleaf Forests and Mixed Coniferous-Broadleaf Forests (Fig. 1, see Gonçalves & Souza, 2013 for a detailed analysis of the studied forests). In the past decades, these forests have suffered human impacts such as logging and clear-cut, which reduced its distribution and increased fragmentation (Souza et al., 2012). Forest structure and floristic composition are distinct between the two forest types and the presence of the coniferous species *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae) characterizes Mixed Forests (Veloso, Rangel Filho, & Lima, 1991; Gonçalves & Souza, 2013). This large emergent tree grows amongst evergreen, tropical and deciduous trees, reaching heights of 25-50m (Teixeira, Coura-Neto, Pastore, & Rangel Filho, 1986). As it is a dominant feature in the landscape, this type of forest is also known as Araucaria Forest. Moist Mixed Conifer-Broadleaf Forests are mainly located in the North, in areas of increasing elevation. This region shows monthly temperatures under 15°C up to eight months out of the year and annual precipitation above 1 300mm, reaching up to 2 500mm (Teixeira et al., 1986). Broadleaf Forests occur mainly as semi-deciduous or deciduous forests, presenting a canopy height of 25-30m and two distinct physiological conditions: one of high transpiration (summer), when temperature is higher than 20°C , and another with low transpiration (winter), when temperature is inferior to 15°C (Teixeira et al., 1986). A small area of rainforest may be found in the Northeast (included as Broadleaf Forest) and the remaining vegetation is characterized as large patches of grassland that form a grassland-forest gradient.

Biomass estimation: Data used for estimation of forest biomass was obtained from the Rio Grande do Sul Forest Inventory (RSFI), a database created between 1999 and 2001 using

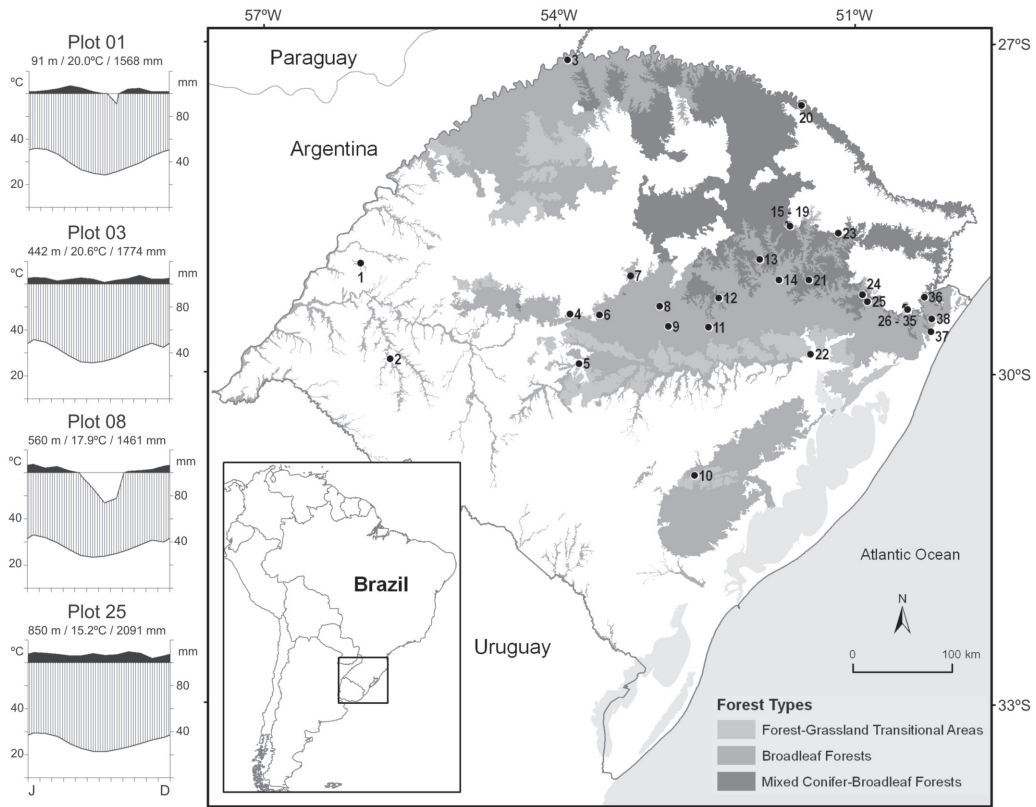


Fig. 1. Distribution of study sites in the vegetation map of subtropical Southern Brazil (Rio Grande do Sul State). Climatic diagrams (Walter and Lieth 1960) show monthly means of temperature (°C, inferior line) and precipitation (mm, upper line). Year averages and total precipitation are shown just above the diagrams. White areas represent grasslands or coastal vegetation.

standard protocols that sampled plots ranging from 0.1-ha to 1-ha in size located throughout the State of Rio Grande do Sul, Southern Brazil (SEMA, 2002). A stratified random sampling procedure was followed to select study sites by watershed and vegetation type (SEMA, 2002). In each plot, all trees with trunk diameter at breast height (DBH) above 9.5cm were measured for height, diameter at breast height and were identified to the species level. A detailed description of the forest fragments, in which the studied plots were established, and their floristic composition was provided by Souza et al. (2012). We selected 38 1-ha plots (100x100m) from the inventory data bank corresponding to native broadleaf (N=16) and

mixed conifer-broadleaf forests (N=22). From these data we calculated stem density, aboveground biomass (AGB) and diversity. Diversity was defined as the effective number of species (true diversities) as suggested by Jost (2006). True diversities were calculated according to the Shannon entropy ($q=1$ in Jost, 2006).

Aboveground biomass was estimated for individual trees in each plot, based on allometric models proposed for different taxonomic groups or forest types. The models use one or more of the following parameters to estimate biomass (expressed in kg): trunk diameter (cm), total height (m) and wood density (g/m^3) of species. The model developed by Chave et al. (2005; 'moist forests' equation) was used for

all angiosperms (except palms) in both forest types (Mixed and Broadleaf). For the palm species *Syagrus romanzoffiana* and *Euterpe edulis*, the model proposed by Pearson, Walker, and Brown (2005) was applied. Contrary to other palm biomass estimation models (Frangi & Lugo, 1985; Moreira-Burger & Delitti, 2010), the one proposed by Pearson et al. (2005) was used due to its generality and range correspondence with our data. With regard to the conifer species *Araucaria angustifolia* and *Podocarpus lambertii*, a modified version of the equation proposed by Sanquetta, Watzlawick, Schumacher, and Mello (2003), corrected for dry weight result, was applied. Wood density values were obtained from global and regional databases (Brown, 1997; Lorenzi, 2002; Chave et al., 2006). Wood density values were gathered for 101 species (61%), which represent 85% of all stems in the database. For species with no record of wood density, genus averages were used (28% of the total of species and 12% of all stems), as in Chave et al. (2005). In a few cases family averages had to be applied (6%). Carbon stock was assumed to be 50% of dry biomass (Balbinot, 2004; Houghton, 2007).

Environmental data: Climate data was compiled for each study site from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The global database uses 1km spatial resolution, for the period of 1950-2000, and provides long term annual and monthly averages of temperature (°C) and precipitation (mm) for locations across the world. The following climate variables were included: total annual precipitation, number of dry months (monthly precipitation <100mm), precipitation seasonality (rainfall coefficient of variation, which represents the annual range of precipitation), annual mean temperature and maximal and minimal temperatures of warmest and coldest months. The identification of soil types was obtained by locating each plot on the regional soil map (scale 1:1 000 000) provided by Streck et al. (2008) using ArcGIS 9.2 (ESRI Inc. 2006). Soil properties (depth, drainage, organic matter, Al³⁺, P, pH,

exchangeable bases, cation exchange capacity and Ki coefficient – a soil weathering index based on the level of decomposition of the clay fraction of the soil, obtained from the SiO₂/Al₂O₃ ratio) were obtained in the Regional Soil Database provided from the Brazilian Ministry of Agriculture (Brasil, 1973) according to the late classification of Streck et al. (2008). Depth and drainage were transformed in dummy variables. Soil cover has not suffered significant changes in the study region during the last decades, and thus there is no reason to suspect that soil data do not correspond to current soil characteristics in the studied plots.

Due to collinearity in both climate and soil data, we used Principal Components Analysis to analyze the effect of climate and soil on aboveground biomass. We first conducted principal components analyses on the set of standardized, log-, square-root- or arcsin-transformed climatic and soil variables to reduce their number into a smaller number of independent, orthogonal composite variables, using Systat 12.0 (Systat, 2007). Only principal components with eigenvalues ≥ 1.0 were retained for analysis (Hair Jr., Anderson, Tatham, & Black, 2005). A Varimax rotation method was employed to minimize the number of variables that have high loadings on each factor (Hair Jr. et al., 2005). Component loadings $>|0.85|$ were considered significant based on sample size (Hair Jr. et al., 2005). Since some of the plots lied close together in the geographical space, they violate the assumption of independence of data (Ter Steege et al., 2003). For these, close plots a central value was selected, excluding similar plots and reducing the number samples used for PCA to a subset of 28 plots (climate data) and 26 plots (soil data) out of the original 38 plots. This procedure was made to reduce overrepresentation of variables on the PCA.

To address the question of the effect of climate and soil on aboveground biomass, we conducted two backward stepwise regressions using the principal components as the independent variables (Systat, 2007). An explanatory model was developed using biomass estimates

as the dependent variable and stem density, species diversity and the significant PCA ordination axes for climate and soil as independent variables. Significance levels of 0.10 and 0.05 were used for variables to enter or leave the model in each step, respectively (Sokal & Rohlf, 1995). A second, applied model was developed using the same variables included in the explanatory model except for the PCA components. Instead, all climate- and soil-related variables that had significant loadings in the factors included in the explanatory model were added as explanatory variables. This applied model was incorporated in order to allow direct estimates of forest biomass in new areas located within the study region, from the variables we studied.

Biomass differences between forest types were assessed using the Mann-Whitney U Test. To evaluate the relative contribution of conifers to the total live biomass, a between-subjects randomized blocks analysis of variance was performed on biomass, with adjustment made for plots identity as random blocks.

The independent variable was biomass with taxonomic group (two levels: angiosperms and conifers) as the main treatment. Plots were explicitly included in the model in order to control for local history, soil type, species composition and other site-specific differences (Sokal & Rohlf, 1995). Aboveground biomass was not spatially autocorrelated (results not shown).

RESULTS

The nine climate variables were reduced to three principal components that explained 92.3% of the variation in the data. The first PCA axis explained 52.3% of the total variance and described a thermal gradient related to elevation (hereafter referred to as the elevation axis). Four variables were significantly correlated with axis one of the PCA: maximum temperature (loading component: 0.98), average temperature (0.98), longitude (0.86), and elevation (-0.88; Fig. 2a). The second axis explained 26.6% of the total variance and described a rainfall gradient (henceforth called

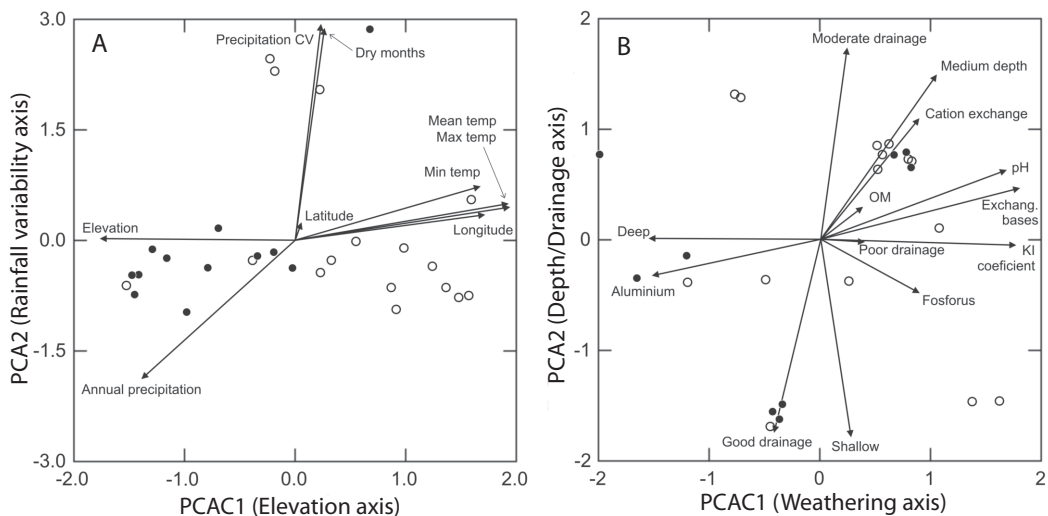


Fig. 2. Ordination by PCA used to summarize climate (a) and soil (b) variables. White circles indicate Broadleaf Forest plots and black circles correspond to Mixed Forest plots. (a) For climate variables, PCA1 explained 52.3% of the total variance, associated the variables mean and maximum temperature, longitude and elevation, describing a gradient related to elevation; PCA2 explained 26.6% of the total variance, described a gradient of rainfall throughout the year and associated the variables rainfall coefficient of variation and number of dry months. (b) For soil variables, PCA1 (33.5% total variance explained) associated the variables exchangeable bases and KI coefficient; and PCA2 (26.6% total variance explained) associated shallow soils, good drainage and moderate drainage.

rainfall variability axis). This axis was related to rainfall coefficient of variation (CV; 0.98) and number of dry months (0.96). The third axis was correlated with just one variable (latitude: -0.98, hereafter, the latitude axis). Plots located in Mixed Forests concentrated to the left of the elevation axis, indicating a positive relationship with altitude and a negative association with temperature and longitude (Fig. 2a). On the other hand, plots located in areas of Broadleaf Forest concentrated to the right of the ordination space, corresponding to higher values of average and maximum temperature and lower values of elevation.

Principal Component Analysis for soil data generated four significant components that explained 88.1% of data variation (Fig. 2b). The first axis was positively correlated to the variables exchangeable bases (0.91) and KI coefficient (0.89), and is hereafter referred to as the weathering axis. The second axis was negatively correlated to shallow soils (-0.90) and good drainage (-0.88) and positively correlated to moderate drainage (0.87), and is henceforth referred to as the depth/drainage axis. The last two axes were positively correlated to only one variable each: poor drainage (0.93) in axis three (poor drainage axis) and organic matter (0.86) in axis four (organic matter axis).

Overall aboveground biomass estimates ranged from 39.0 to 494.5Mg/ha (1Mg=10³kg). Mean aboveground biomass was 195.2Mg/ha (152.8-239.9 bootstrapped 95% CI) and average carbon stock derived from biomass estimates was 97.6Mg C/ha. Mixed Forests presented higher biomass estimates (mean=250.3, 205.5-298.5 bootstrapped 95% CI) than Broadleaf Forests (mean=118.9, 92.0-147.1 bootstrapped 95% CI; U=49.0, p<0.001). In Mixed Forests, biomass was significantly related to taxonomic group ($F_{37,24420}=99.98$, p<0.001), with conifers presenting significantly higher biomass than angiosperms. Mean aboveground biomass for conifers was 0.87Mg/ha while angiosperms averaged 0.22Mg/ha. Among conifers, *Araucaria angustifolia* contributed with 98% of AGB, while *Podocarpus lamberti* contributed

with only 2%. Palms contributed with 63.9Mg (<0.5%) to total biomass estimates.

The explanatory multiple regression model selected five variables associated with aboveground biomass, explaining 50.7% of the total variation in AGB (adjusted- $r^2=0.507$). Biomass estimates were positively related to stem density and elevation, and negatively related to latitude, diversity and the organic matter axis ($Y_{\log \text{ biomass}} = 0.03(0.48)x_{\text{sqrt stem density}} + 0.11(0.35)x_{\text{elevation axis}} - 0.22(-0.85)x_{\text{latitude axis}} - 0.03(-0.38)x_{\text{diversity}} - 0.09(-0.34)x_{\text{organic matter axis}} + 1.70$; $F_{5,32}=8.62$, p<0.001; $r^2=0.507$). Note that both elevation and latitude were negatively loaded on their respective PCA axis (Fig. 2). The elevation axis contributed more to the model than any other variable, as seen by the values of the standardized regression coefficients (in the above equation, in parentheses; Fig. 3). The applied regression model explained 54.7% of the total variation in biomass estimates ($Y_{\log \text{ biomass}} = 0.001(0.91)x_{\text{elevation}} + 0.03(0.44)x_{\text{sqrt stem density}} - 0.03(-0.43)x_{\text{diversity}} - 2.76(-0.31)x_{\text{organic matter}} + 1.82$; $F_{4,33}=12.15$, p<0.001; $r^2=0.547$). The main variables included in the explanatory multiple regression model were maintained in the applied model. It is worth noting that each explanatory variable included in this model was correlated with a different PCA axis, what makes them statistically independent. One outlier point was present in both models. It was not removed from the analysis because it represented a natural extreme of variation. Variogram analyses revealed lack of spatial structure in aboveground biomass (data not shown; Fig. 4).

DISCUSSION

The mean biomass estimates obtained in this study lie in the range of values obtained for tropical and subtropical forests. For tropical rain forests, mean aboveground biomass estimates range from 239Mg/ha to 325Mg/ha (DeWalt & Chave, 2004; Laurance et al., 1999; Nascimento & Laurance, 2002). Studies performed in the Atlantic Forest of Argentina and Brazil found mean estimates ranging from 240 to 334Mg/ha (Rolim et al., 2005;

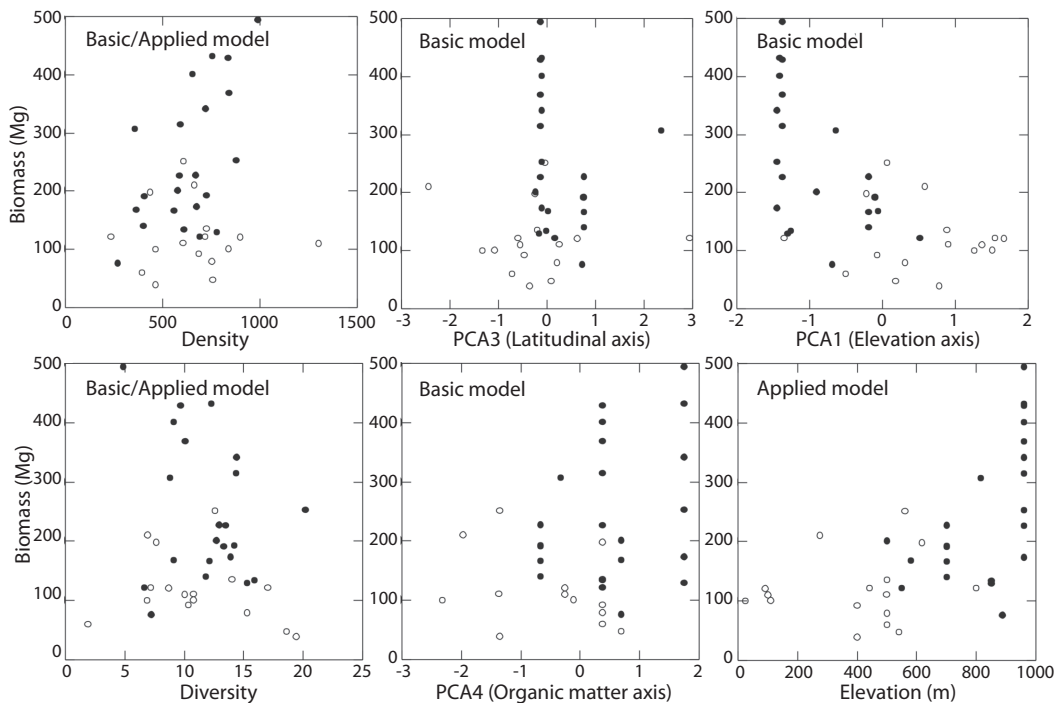


Fig. 3. Relationship between aboveground biomass estimates and the environmental and biotic variables included in the explanatory (basic) and applied models (see text). The variable of greater importance to the regression model is the elevation axis, which is associated with greater values of temperature (maximum and mean) and longitude and lower values of elevation. Values are based on 1-ha plots, white circles indicate Broadleaf Forest plots and black circles correspond to Mixed Forest plots.

Gasparri et al., 2008; Alves et al., 2010). Our study showed mean biomass values for Mixed Forests (250.3Mg/ha) in the range found in the studies listed above, as well as the values of 220Mg/ha proposed for subtropical humid forests by the Intergovernmental Panel on Climate Change (IPCC, 2006) and 212Mg/ha estimated for forests in Brazil by the Food and Agriculture Organization of the United Nations (FAO, 2009). Specifically for Broadleaf Forests located at lower elevations of Southernmost Brazil, results showed a low biomass mean estimate (118.9Mg/ha).

The high spatial local variability found in our data is not unusual for tropical and subtropical moist forests. Local variability is caused by the presence/absence of large trees (DBH ≥ 70 cm), which may alter AGB estimates at about 30 to 40% (Brown, 2002). Even plots with low stem density may show high biomass

estimates due to the presence of individuals of large and very large DBH (around 100cm, but see Clark & Clark, 2000). In our study, the plot that accounted for the lowest stem density, large trees represented only 4% of all individuals, but accounted for 37% of the total biomass. Data on regional variability, on the other hand, may be needed to detect the effects of environmental factors, which have strong effects on aboveground biomass (Clark & Clark, 2000). The ordination axis related to elevation had a strong negative relationship with altitude and low values of this axis reflect an increase in elevation and a decrease in temperature (as well as longitude). This indicates increasing biomass towards higher altitudes (in the Northeast), as suggested by Souza et al. (2012). Increased altitudes are accompanied by cooler temperatures and elevated rainfall, partially fulfilling our first expectation of greater biomass in

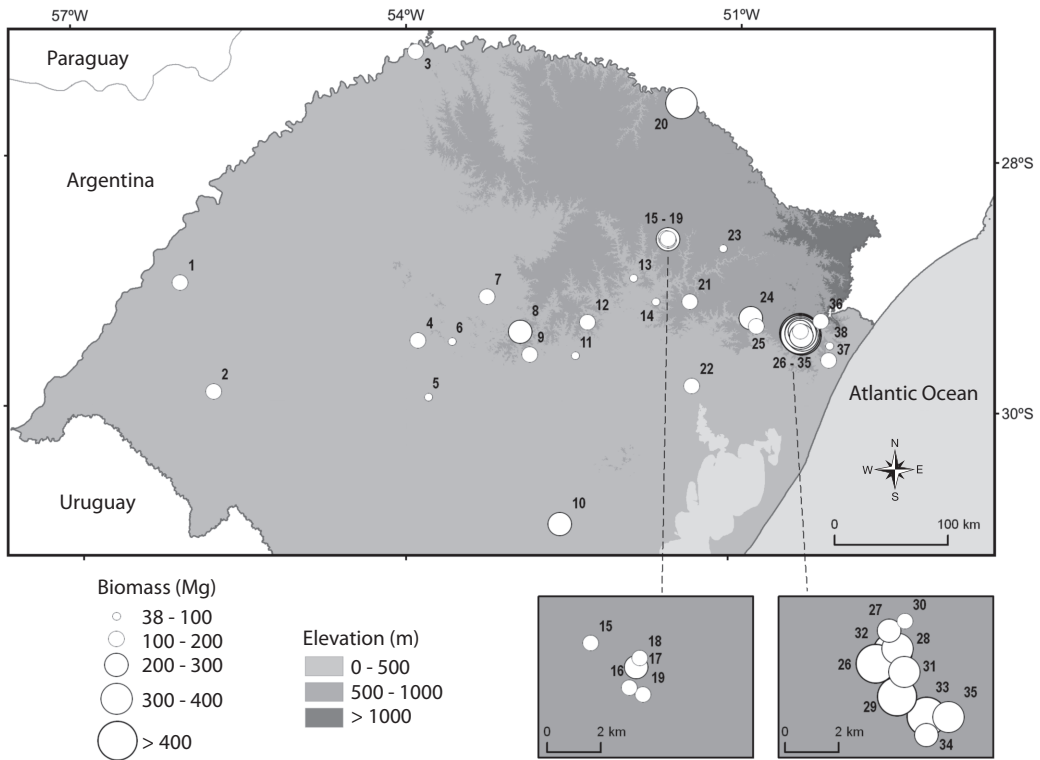


Fig. 4. Distribution of study plots in the altitudinal gradient of subtropical Southern Brazil. Circles diameter indicate biomass estimates (Mg/ha).

areas of homogeneous rainfall throughout the year. A similar pattern is found in the Amazon forest, where monthly distribution of rainfall is believed to be the most important factor influencing biomass (Saatchi et al., 2007).

However, the results from the multiple regressions resulted opposite to other studies which stated that the increase in altitude reduces biomass due to decreasing photosynthesis rates and low wood increment (Tanner et al., 1998; Raich et al., 2006). However, a recent study performed in Southeast Brazil (Alves et al., 2010), showed a positive correlation between aboveground biomass and increasing elevation, agreeing with the present study. Alves et al. (2010) credited this relation to the contribution of very large stems, growing on steeper slopes of higher altitudes, to the total aboveground biomass. Slope angle does not seem to be the reason of the variation in our

case, but contribution of trees with DBH>50cm to biomass estimates at higher altitudes did indeed represent an important factor (data not shown). The increase of biomass estimates towards higher elevations results in differences between forest types. Apart from the floristic and structural differences found in Broadleaf and Mixed Coniferous Broadleaf Forests, the most important contribution to biomass seems to be the occurrence of the species *Araucaria angustifolia*, a dominant species in Mixed Forests of the region, fulfilling Expectation (3). Results from the randomized blocks, ANOVA showed a significant difference between biomass of conifers and angiosperms, mainly due to the contribution of *A. angustifolia*. As many conifers, trees of this species accumulate high biomass, mainly stored in the wood trunk (Sanquetta et al., 2003). Temperate coniferous forests around the world are one of the

most carbon dense forests, presenting mean values of 377Mg/ha in regions of temperate climate (Keith et al., 2009). In the study plots where *A. angustifolia* was abundant, its biomass accounted for more than 70% of the total AGB of the sample.

The proposed model for these Subtropical Forests indicated, aside from altitude, the influence of stem density, diversity and organic matter. Our third expectation (positive correlation between stem density and biomass) was thus confirmed. The negative effect of species diversity in the estimated biomass is in contradiction with Expectation (2). Experimental studies performed in grasslands (Tilman et al., 2002; Cardinale et al., 2007) identified a positive effect of species richness and diversity on biomass. This pattern might not hold in forest ecosystems and further studies should be carried out to evaluate the generality of our findings. Species composition, on the other hand, might be an important influence on biomass accumulation, since species-specific growth patterns lead to differential biomass accumulation (Bunker et al., 2005; Chave et al., 2006). Finally, in some tropical forests, soil organic matter accumulates due to nutrient limitation caused by decreased decomposition rates (Schoor, 2003). In our study, the negative effect of organic matter on biomass may be explained by increased decomposition and nutrient availability, which enables higher productivity.

As mentioned above, the studied forests have suffered human impacts such as logging and clear-cut, which reduced its distribution and increased fragmentation (Souza et al., 2012). Such history may have influenced our results. Logging of *Araucaria angustifolia* trees and many other dense wood native species (Albano Backes, pers. comm.) probably reduced mixed forest biomass stocks. The combination and interaction of environmental conditions, land use history, species morphological characteristics and disturbance regimes described above may influence the estimated carbon stock in these forests (Keith et al., 2009).

The results obtained in our study show the spatial and local variability in aboveground

forest biomass in subtropical forests. These results are important in developing country-based biomass maps and may help improve remote sensing estimates based on satellite images (Gibbs, Brown, Niles, & Foley, 2007; Saatchi et al., 2011). A significant variability in biomass estimates was found between forest types in a relatively short distance, highlighting the importance of the inclusion of regional and local data in satellite image estimates for large areas (Baccini et al., 2008). The present study presents an outlook of aboveground biomass distribution in forests in subtropical Southern Brazil and highlights the main factors affecting the regional variability of biomass. By the results obtained, it suggests the potential for biomass storage and carbon sequestration of subtropical montane forests and emphasizes the role of the species *Araucaria angustifolia* in biomass and carbon storage in the region. This threatened species (critically endangered according to IUCN (2010)) is one of the most important features in higher altitudes of the Atlantic Forest and is responsible for maintaining an elevated number of species of fauna and flora that are associated with it (Fonseca et al., 2009). Due to climate change, the current focus on biomass storage and carbon sequestration may influence on the conservation of Mixed Forest (*Araucaria* Forest) areas, since conserving these forests from deforestation could maintain biodiversity and improve carbon stock (Keith et al., 2009). Given the few studies of aboveground biomass in subtropical forests, when compared to other tropical forests, the aboveground estimates presented here are one of the first attempts to estimate subtropical biomass at broader scales. This may also stimulate the development of new and fitter equations for these forest formations, improving future biomass estimates.

ACKNOWLEDGMENTS

Financial support was provided by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES (grant given to the first author). We would like to thank the Programa

de Pós-Graduação em Ecologia (coordinated by José Luiz de Attayde) of Universidade Federal do Rio Grande do Norte for the help with publishing costs. We would like to thank Rio Grande do Sul State Government (SEMA/RS) for providing the Forest Inventory Database, Heinrich Hasenack and Lúcio Lucatelli for the contribution in developing the maps and Erivelton Tomazzoni for help with data gathering. We are grateful to two anonymous reviewers for their comments on a previous version of this paper.

RESUMEN

Variación de la biomasa forestal en el sur de Brasil: impacto de los árboles de Araucaria. Una variedad de factores ambientales y bióticos determinan el crecimiento de la vegetación y afectan la acumulación de biomasa vegetal. Desde la temperatura hasta la composición de especies, en los ecosistemas forestales el almacenamiento de la biomasa aérea se ve influenciada por una serie de variables, razón por la cual generalmente presenta una alta variabilidad espacial. De acuerdo a esto, el objetivo del estudio es analizar las variables que afectan la biomasa aérea (en Inglés, *aboveground forest biomass* - AGB) en los bosques húmedos subtropicales del sur de Brasil y analizar su distribución espacial. Para el estudio se utilizaron los datos de un inventario forestal realizado en el estado de Rio Grande del Sur, sur de Brasil. Se evaluaron bosques de hoja ancha (*Broadleaf forests*) y bosques mixtos de hoja ancha y coníferas (*Mixed Coniferous-Broadleaf forests*). Además, se tomaron muestras de 38 parcelas de 1 ha y para la estimación de la biomasa se incluyeron todos los árboles con DAP ≥ 9.5 cm. Los valores para la biomasa aérea se obtuvieron con ecuaciones alométricas publicadas. Las variables ambientales y bióticas (altitud, precipitación, temperatura, suelo, densidad de los troncos y diversidad de especies) se obtuvieron de la literatura o se han calculado a partir del conjunto de datos. Para el conjunto de datos, el AGB medio fue 195.2Mg/ha. Las estimaciones difieren entre los bosques de hoja ancha y los bosques mixtos de hoja ancha y coníferas: el AGB promedio fue menor en los bosques de hoja ancha ($AGB_{BF}=118.9$ Mg/ha) en comparación con los bosques mixtos ($AGB_{MF}=250.3$ Mg/ha). Hubo una alta variabilidad espacial y local en la base de datos, incluso dentro de los tipos de bosques. Esta condición es normal en los bosques tropicales y por lo general se atribuye a la presencia de grandes árboles. La regresión múltiple fue influenciada principalmente por la altitud y explicó 50.7% de la variación en AGB. La densidad, diversidad y materia orgánica también influyeron en la variación de biomasa. Los resultados mostraron una relación positiva entre la biomasa sobre el suelo y la altitud. Por lo tanto,

los valores más altos de AGB se encuentran en altitudes mayores y se someten a temperaturas más bajas y un clima más húmedo. Parece que hay una importante contribución de las coníferas *Araucaria angustifolia* en las parcelas de bosques mixto, ya que tienen una biomasa significativamente mayor que las especies de angiospermas. En Brasil, esta especie en peligro de extinción es parte de un bosque de gran diversidad (Bosque de Araucaria) y tiene el potencial de almacenamiento de la biomasa. Los resultados del presente estudio muestran la variabilidad espacial y local de la biomasa aérea en los bosques subtropicales, destacan la importancia de estos ecosistemas en el almacenamiento global del carbono, y estimulan la mejora de futuras estimaciones de biomasa.

Palabras clave: métodos indirectos, reservas de carbono, modelo de regresión, bosques de hoja caduca, distribución espacial.

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