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REVIEW ARTICLE

Biomass and carbon in subtropical forests: Overview of determinants, quantification methods and estimates

Biomassa e carbono em florestas subtropicais: determinantes, métodos de quantificação e estimativas

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Abstract

The study of biomass is an important tool to evaluate the amount of carbon stored in ecosystems. Biomass accumulation is determined by many factors that affect community structure and productivity but its quantification presents a challenge due to its high spatial variation. The main purposes of this paper are to describe the factors influencing tree biomass, indicate the main methods used in quantification and show the spatial distribution and lack of estimates in subtropical forests. In forest ecosystems, aboveground biomass is mostly comprised of trees. Its storage is dependent of many environmental and biotic factors, including temperature, rainfall, soil characteristics and species composition. The quantification is usually made by direct weighing in the field or estimated through allometric equations. Destructive methods require cutting and weighing the plant material, encompassing a large labor force and a long period of fieldwork. Indirect methods on the other side are based on estimates obtained through allometric mathematical models or remote sensing techniques that rely on data of tree parameters collected from the community. Aboveground biomass estimates vary considerably across regions and forest types. Tropical and temperate forests concentrate the majority of biomass studies and few of these have evaluated aboveground biomass in subtropical forests at broader scale. These forests have been shown to have high biodiversity and great potential for carbon accumulation. Studies that focus on evaluating the factors that affect biomass storage at different locations and that aim at developing and improving regional allometric equations are important for making reliable estimates of forest ecosystems. Finally establishing long-term study sites will provide relevant data for monitoring biomass accumulation and shifts through time.

Key words: environmental variables, allometric models, biomass estimates, spatial distribution.

Resumo

O estudo da biomassa é uma ferramenta importante para avaliar a quantidade de carbono acumulado nos ecossistemas. O acúmulo de biomassa é determinado por inúmeros fatores que afetam a estrutura da comunidade e a produtividade, mas sua quantificação representa um desafio devido à alta variação espacial. Os principais objetivos deste trabalho são descrever os fatores que influenciam a biomassa arbórea, indicar os principais métodos usados para quantificá-la e mostrar a distribuição espacial e falta de estimativas em florestas subtropicais. Em ecossistemas florestais, a biomassa acima do solo é composta predominantemente de árvores. Seu acúmulo é dependente de inúmeros fatores ambientais e bióticos, incluindo temperatura, precipitação, características do solo e composição de espécies. A quantificação é geralmente realizada pela pesagem do material

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em campo ou estimada através de equações alométricas. Métodos destrutivos exigem corte e pesagem do material vegetal, abrangendo uma grande força de trabalho e um longo período em campo. Métodos indiretos, por outro lado, são baseados em estimativas obtidas através de modelos alométricos ou técnicas de sensoriamento remoto, que dependem de dados de parâmetros arbóreos coletados na comunidade. Estimativas de biomassa acima do solo variam consideravelmente entre regiões e entre tipos florestais. Florestas tropicais e temperadas concentram a maior parte dos estudos e poucos são aqueles que avaliaram a biomassa acima do solo em florestas subtropicais em ampla escala. Essas florestas apresentam alta biodiversidade e grande potencial para acúmulo de biomassa. Estudos que foquem na avaliação de fatores que afetam o estoque de biomassa em diferentes regiões e que objetivem o desenvolvimento e o aprimoramento de equações alométricas regionais são importantes para estimar de forma confiável a biomassa em ecossistemas florestais. Por fim, a definição de áreas de estudo de longa duração poderá fornecer dados importantes para o monitoramento do acúmulo de biomassa e suas mudanças ao longo do tempo.

Palavras-chave: variáveis ambientais; modelos alométricos; estimativas de biomassa; distribuição espacial.

Introduction

The study of standing biomass is one of the main tools used to evaluate the amount of carbon stored in ecosystems and assess forest productivity and net carbon flux (Brown 2002; Houghton, 2003a). Although mainly determined by community structure and disturbance history (Clark and Clark, 2000; Houghton, 2005), forest aboveground biomass (AGB) is also influenced by biotic and abiotic factors acting on tree height, stem density, basal area and species abundance (Saatchi *et al*., 2007; Stegen *et al*., 2011). These complex effects are further complicated by the fact that the community size-frequency distribution of trees (Clark and Clark, 2000; Brown, 2002) and stand successional stage (Baker *et al*., 2004b) can also affect the evaluation of carbon storage.

The high spatial variability in biomass stocks both within formations and across regions (DeWalt and Chave, 2004) presents a challenge for measuring this biomass. Different methods are available for assessing biomass in forest ecosystems, from destructive to allometric-based models (Chave *et al*., 2001; Brown, 2002), which show different accuracy and provide different results (true values x estimates). Our purpose here is to identify the different factors influencing biomass accumulation and review the main methods used to calculate biomass in forest ecosystems. We also aim to compare the distribution of biomass estimates in high diversity subtropical forests in different locations, a vegetation type poorly studied regarding biomass/carbon stock.

Forest biomass and carbon storage

Biomass accumulation is determined by net primary productivity, which consists of what is produced through photosynthesis and lost in plant respiration (Clark *et al.,* 2001). Compared to other terrestrial vegetation types, forests have higher rates of carbon fixation, due to greater accumulation in trees (Houghton, 2007). Disturbances such as forest cutting and wood extraction affect the balance of this element in these ecosystems because forests become sources of CO_2 to the atmosphere (Brown, 2002). 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). In natural conditions, carbon release is caused by respiration and decomposition (Houghton, 2007). Human activities such as forest removal and fossil fuel emission are major sources of CO_2, causing changes in global climate and atmospheric composition (Brown *et al*., 1989). Long-term biomass evaluation across world regions may help monitor carbon stocks and identify the impact of these changes in natural ecosystems.

In forests, plant biomass is defined as the quantity of plant material expressed in mass units per unit area (Brown, 1997; Araújo *et al*., 1999). Aboveground plant biomass found in forests is mostly comprised of trees of different sizes and also of shrubs and herbs in the understory. Trees with diameter at breast height (DBH) higher than 10 cm comprise the vast majority of forest biomass, in many cases exceeding 90% of the total aboveground biomass (Clark *et al*., 2001). These results come from the fact that wood is an important carbon reservoir in terrestrial ecosystems and represents around 50% of forest biomass (Balbinot, 2004; Houghton, 2007). Wood density is also a factor that can influence the amount of biomass stored in forests since it is an indicator of life history strategies that vary with ecosystem conditions (Muller-Landau, 2004). Wood density is influenced by tree species (Henry *et al*., 2010) and inversely related with species light demand (Baker *et al*., 2004b) so that species that need more radiation, such as pioneer species, have lower wood density than shade tolerant species. Pioneer species allocate resources on growth in detriment of the strength of the trunk (Nogueira *et al*., 2005) while secondary species that usually have slower growth rates allocate energy on support and resistance to predator and pathogens (Chave and Webb, 2006). Thus the change in species composition during succession also contributes to the variation in biomass accumulation, as fast growing pioneer species are slowly replaced by slow growth secondary species (Chave and Webb, 2006). This fact also helps explain why forest productivity is high at early stages of forest development and decreases as forests age (Pregitzer and Euskirchen, 2004; Gower *et al*., 1996), since the community is composed of pioneer fast growing species. Biomass storage, on the other hand, increases in advanced stages (Pregitzer and Euskirchen, 2004) where there is a marked presence of large diameter trees that accumulate higher biomass (Baker *et al*., 2004b) and a high frequency of slow growth species.

The production and accumulation of plant biomass is largely affected by the factors that influence productivity, such as latitude, altitude, precipitation and temperature. Regional or even local differences may influence a range of other factors, from variations in temperature, rainfall seasonality and soil type, to structure, floristic composition and disturbance regimes. Many studies have focused on the relationship between environmental variables and biomass production, indicating positive correlation between temperature, rainfall homogeneity (reduced seasonality) and soil fertility, with productivity, therefore elevating biomass storage (Laurance *et al*., 1999; Ter Steege *et al*., 2003; DeWalt and Chave, 2004; Raich *et al*., 2006; Saatchi *et al*., 2007). This may be due to adequate conditions in water and nutrient availability, apart from higher photosynthetic rates for biomass production. The analysis of forest carbon storage around the world identified that temperate forests located in regions of moderate temperatures and precipitation rates present greater values of carbon stock (Keith *et al*., 2009), since this condition provides rapid growth and lower decomposition rates. At large geographic scale, Stegen *et al*. (2011) indicated that the most important factor that determines forest biomass is maximum individual biomass, which in turn is determined in part by water deficit rather than the abiotic conditions cited before.

Aside from environmental determinants, biotic factors also influence biomass accumulation in forests. Community diversity and species richness would affect productivity through functional diversity and ecosystem structure, consequently influencing the amount of carbon stored in these ecosystems (Catovsky *et al*., 2002). Experiments that investigated the effect of floristic composition in productivity in grasslands suggest higher biomass accumulation in richer communities (Reich *et al*., 2001; Tilman *et al*., 2002). 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. The most likely explanation to these findings relates to the range in community functional groups (Reich *et al*., 2001), since niche complementarity would result in better resource use efficiency (Naeem, 2002). In the case of forest ecosystems, evidence suggests that carbon storage in tropical forests is dependent on the existing species composition (Bunker *et al*., 2005). Although there are a number of grassland studies relating biomass to species diversity (Tilman *et al*., 2002; Van Ruijven and Berendse, 2009; Hector *et al*., 2011) this pattern is not clear for forest ecosystems.

Quantification methods

Different approaches exist to quantify plant biomass in forest ecosystems. Destructive methods require cutting and weighing the organic plant material existing in the selected community (Chave *et al*., 2001), whether it is applied to a specific plant group (tree, shrubs, herbs or epiphytes) or the whole community. Indirect methods, on the other hand, are based on estimates obtained through allometric mathematical models or remote sensing data (Brown, 2002) and do not require direct impact in the forest. Advantages and disadvantages are inherent in both approaches and are related to the efficiency of data gathering, definition of the model or technique to be used and the selection of the study areas (Brown, 2002; Houghton, 2005). An additional source of error is that the selected studied areas might not reflect the full range of forest biomass variability (Chave *et al*., 2001; Houghton, 2005). This is particularly likely because researchers tend to favor more conserved or accessible areas (Houghton, 2005; Silveira *et al*., 2008). Silveira *et al*. (2008) described in detail different equations for obtaining forest biomass and carbon estimates, encompassing different forest types around the world. Goetz *et al*. (2009) describes different remote sensing techniques used to obtain biomass/carbon maps.

Destructive methods used to measure plant biomass require a great effort of suppression and weighing the plant material, encompassing a large labor force and a long period of fieldwork (Clark *et al*., 2001; Houghton, 2005). Although the removal of forest coverage is a method of very significant impact it is an imperative process for developing and calibrating estimates in indirect methods (Brown *et al*., 1989; Chave *et al*., 2001). In this sense, many researchers in Brazil have performed this type of activity in the Amazon region (Araújo *et al*., 1999; Nogueira *et al*., 2008) and in the Atlantic Forest (Burger and Delitti, 2008; Socher *et al*., 2008; Silveira, 2009; Moreira-Burger and Delitti, 2010). Restrictions to the use of destructive methods are due to the large effort of data collection and required equipment, apart from the strong impact in the environment. On the other hand, this approach may be the most reliable method for measuring tree biomass since the weighing of plant material considers irregularities in the arboreal structure (deformations, attacks of pathogens, hollow trunks, for example), which may affect the amount of stored biomass and carbon (Nogueira *et al*., 2006). A problem inherent in the method is that since it requires a great amount of work and is time consuming (Houghton, 2005), data collected may not reflect all the diameter range presented in the forest (Brown, 2002), mainly because very large trees are not frequent enough to be sufficiently representative in the equations.

In order to facilitate the achievement of plant biomass estimates, non destructive methods were developed to evaluate biomass and carbon stock. One of these methods consists of the use of mathematical models, which use allometric equations to establish relations between tree parameters and plant biomass (Brown, 2002). A large number of models available in the literature consider data from forest inventories that present data of trunk diameter and total height (Brown *et al*., 1989; Frangi and Lugo, 1985; Chave *et al*., 2005). Chave *et al*. (2008) describe through results of other authors that the debate concerning the best models to measure aboveground biomass revolve around the accuracy of trunk diameter measurements, the allometric equation selected and the spatial area covered by the forest census (sample size). Different errors caused by incorrect measures, sampling and uncertainty in model selection may affect the power of the estimation. A study performed in tropical forests around the world evaluated the importance of predictive variables (trunk diameter, height and wood density) for application in allometric equations (Chave *et al*., 2005). The results indicated that trunk diameter is the main factor related to tree biomass and that the inclusion of the variable wood density increases model reliability, especially in high diversity and species-rich forests (as is the case of tropical forests). Wood density may be important in considering regional differences between forests and results suggest that it may explain up to 30% of the aboveground biomass variation (Baker *et al*., 2004a; Vieira *et al*., 2008). Height, although not an essential element in the previsions, increases the precision of the model (Brown, 2002) as it considers architectural differences among individuals, reducing uncertainty of biomass estimates (Feldpausch *et al*., 2012).

It is important to highlight that forests around the world have different environmental characteristics. This implies that biomass estimation among different forest types (dry and moist, tropical and subtropical forests, for example) should be evaluated in the most adequate way. Preference should be given to the use of equations developed in areas with similar characteristics, increasing model efficiency (Chave *et al*., 2005; Burger and Delitti, 2008). The most robust models used for forest biomass estimation, which considered a satisfactory number of sample units and a larger range of elevated trunk diameter classes (very large trees), were obtained for tropical forests (Frangi and Lugo, 1985; Chave *et al*., 2005). In other regions, as is the case for subtropical forests and specially the Atlantic Forest, most of the proposed equations part from a reduced number of cut trees (Vogel *et al*., 2006; Burger and Delitti, 2008) which could result in errors in estimates (Chave *et al*., 2001). This often results in low representation of large diameter trees that hold for large biomass storage. However even in the absence of specific allometric models for these forests, pan-tropical equations may be used to estimate biomass in a reliable way, provided that values of trunk diameter, height and wood density are in the range proposed in the model (Chave *et al*., 2005; Vieira *et al*., 2008). Chave *et al*. (2005) emphasize that equations used for tropical forests should be used only for broadleaf tree species and that different models should hold for the presence of conifers and palms whose morphological characteristics differ significantly from other species. Finally, in spite of the fact that studies with live aboveground biomass consider mostly the tree component of vegetation, there is a fraction of this biomass that is represented by lianas, epiphytes, palms, shrubs and small trees (Vieira *et al*., 2008) and also by the herbaceous stratum of the vegetation. Trees with DBH above 10 cm correspond to the greatest portion of forest biomass (Clark *et al*., 2001; Keller *et al*., 2001) and consequently are indispensable for forest estimates. The contribution of lianas, palms and small diameter trees however should not be disregarded, since these groups may contribute to more than 10% of total biomass by hectare (DeWalt and Chave, 2004; Vieira *et al*., 2008).

Patterns at distinct geographical scales

The quantification of plant biomass is of great relevance in estimating carbon stock stored in forest ecosystems. A great variability in biomass estimates is found in tropical and subtropical forests, mainly due to high species diversity and different environmental conditions that affect plant growth (Clark and Clark, 2000). The history of natural and human disturbance has a direct effect on the different existing successional stages, contributing to this variability (Houghton, 2005). The distribution of biomass estimates varies among world regions and also between forest types. According to a study performed in 2000 by the Food and Agriculture Organization of the United Nations (FAO, 2001), the regions that have greater aboveground biomass are South America (42.7%), Africa (16.8%) and Europe (14.5%). In the same report, over a third of the 420 billion tones of aboveground biomass in forest ecosystems around the world are located in South America and 27% only in Brazil. Besides tropical forests, the great contribution of temperate forests to these projections should not be underestimated, where high values of biomass and carbon storage are found (Keith *et al*., 2009). According to the FAO (2001), global forest aboveground biomass is estimated to be 109 Mg ha^{-1} (1 Mg = 10^{6} g). South America has the higher estimate, evaluated in 128 Mg ha^{-1} (FAO, 2001). The estimates obtained for tropical forests range from 225 to 399 Mg ha^{-1}, taking into account forests in Africa, Asia and in Neotropical Forests, in this case the Amazon Forest (Clark and Clark, 2000). Estimates in the South of the Atlantic Forest have a similar pattern, ranging from 256 to 334 Mg ha^{-1} (Rolim *et al*., 2005; Gasparri *et al*., 2008). Normally these values refer only to trees with DBH greater than 10 cm. Unfortunately the majority of biomass studies are concentrated in tropical or temperate forests with a lack of studies in subtropical forests (Lin *et al*., 2012). Studies in subtropical forests in China presented average biomass estimates of 164 Mg ha^{-1} (Fang *et al*., 1998) and 223 Mg ha^{-1} (Lin *et al*., 2012). Frangi and Lugo (1985) estimated biomass in a wet subtropical forest in Puerto Rico in 285Mg ha^{-1}. In southern Brazil (Rosenfield and Souza, n.d.), mean forest aboveground biomass estimates was 250 Mg ha^{-1} for Mixed Forests (corresponding to the distribution of Araucaria Forest, according to the Brazilian classification of Teixeira *et al*. (1986) and 119 Mg ha^{-1} for Broadleaf Forests (corresponding to Atlantic Forest and Seasonal Deciduous and Semideciduous Forests). The average for the region, considering both forest types resulted in 195 Mg ha^{-1} (equivalent to 97.5 MgC ha^{-1}). Other estimates obtained in nearby Seasonal Forests indicate mean tree biomass between 141 and 210 Mg ha^{-1} (Brun, 2004; Vogel *et al.*, 2006) and for Araucaria Forest between 169 Mg ha^{-1} and 398 Mg ha^{-1} (Watzlawick *et al*., 2002).

A map of carbon stocks for tropical regions was developed by Saatchi *et al.* (2011), which resulted in an estimate of global stored aboveground carbon of 193 PgC (1 Pg = 10^{15} g). Latin America accounted for 49% of the total, Southeast Asia, 26%, and sub-Saharan Africa, 25%. Estimates for Brazil are 62 PgC (Saatchi *et al*., 2011), which include biomass estimates for all vegetational types in the country (tropical forests and the *cerrado* and *caatinga* biomes). Following the results of Rosenfield and Souza (n.d.) estimation of total aboveground biomass and carbon stock in southern Brazil (State of Rio Grande do Sul) may be performed using the area covered by forests (Cordeiro and Hasenack, 2009). The State forested area corresponds to $9.3 \cdot 10^{6}$ ha of which $6.3 \cdot 10^{6}$ ha are covered by Broadleaf Forests and $3.0 \cdot 10^{6}$ ha, by Mixed Forests. Considering that carbon estimates differ among forest types (59.5 MgC ha^{-1} for Broadleaf Forests and 125.0 MgC ha^{-1} for Mixed Forests), carbon stock estimated for each forest is 0.37 PgC, resulting in 0.74 Pg of forest carbon in the State. This represents less than 1% of Brazilian carbon stock, estimated to be 49.3 PgC (FAO, 2009), which includes forested areas of the Amazon and the tropical Atlantic Forest. In other subtropical regions, results of carbon pools were similar: in the Atlantic Forest of Argentina (Gasparri *et al*., 2008), carbon stock was estimated in 0.26 Pg C covering a forested area of $1.4 \cdot 10^{6}$ ha (182.9 MgC ha^{-1}, also including the contribution of understory vegetation); and in China (Piao *et al*., 2005), evergreen broadleaved forests (including tropical and subtropical forests) resulted in an estimated carbon of 1.47 Pg C, covering an area of $27.97 \cdot 10^{6}$ ha (52,6 MgC ha^{-1}).

The values of biomass and carbon stock presented here are of great importance since they refer to estimates obtained in subtropical forests, a vegetation type poorly studied relative to tropical forests. Subtropical forests have been shown to have high biodiversity and great potential for carbon accumulation. Studies that focus on evaluating the factors that affect biomass storage at different locations and that aim at developing and improving allometric equations are important for making reliable estimates of forest ecosystems. In this way, destructive methods may be needed to accurately quantify biomass and develop specific and more robust models for these regions. Given the scenario of land use, deforestation, unsustainable exploitation of natural forest resources in increasingly fragmented landscapes, growing amounts of carbon dioxide are being released to the atmosphere (Houghton, 2003b; Clark, 2004). In this context it is important to establish long-term study sites that provide data on biomass estimates and of shifts in biomass stocks and carbon balance through time.

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