

Disentangling the factors that contribute to variation in forest biomass increments in the mid-subtropical forests of China

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Abstract Mid-subtropical forests are the main vegetation type of global terrestrial biomes, and are critical for maintaining the global carbon balance. However, estimates of forest biomass increment in mid-subtropical forests remain highly uncertain. It is critically important to determine the relative importance of different biotic and abiotic factors between plants and soil, particularly with respect to their influence on plant regrowth. Consequently, it is necessary to quantitatively characterize the dynamic

spatiotemporal distribution of forest carbon sinks at a regional scale. This study used a large, long-term dataset in a boosted regression tree (BRT) model to determine the major components that quantitatively control forest biomass increments in a mid-subtropical forested region (Wuyishan National Nature Reserve, China). Long-term, stand-level data were used to derive the forest biomass increment, with the BRT model being applied to quantify the relative contributions of various biotic and abiotic variables to forest biomass increment. Our data show that total biomass (t) increased from 4.62×10^6 to 5.30×10^6 t between 1988 and 2010, and that the mean biomass increased from 80.19 ± 0.39 t ha⁻¹ (mean \pm standard error) to 94.33 ± 0.41 t ha⁻¹ in the study region. The major factors that controlled biomass (in decreasing order of importance) were the stand, topography, and soil. Stand density was initially the most important stand factor, while elevation was the most important topographic factor. Soil factors were important for forest biomass increment but have a much weaker influence compared to the other two controlling factors. These results provide baseline information about the practical utility of spatial interpolation

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methods for mapping forest biomass increments at regional scales.

Keywords Spatiotemporal variation · Stand-level biomass increment · Mid-subtropical forest · Boosted regression tree · Biotic factor · Abiotic factor

Introduction

Mid-subtropical forests represent the main forest vegetation type of global terrestrial biomes, and contain many forest species with high biomass and productivity at the regional scale. Consequently, these forests are important for maintaining the global carbon balance (Zeng et al. 2013; Shi et al. 2015). However, there remains a large degree of uncertainty associated with estimating forest biomass increment in mid-subtropical forests (Yang et al. 2005; Pan et al. 2011). The lack of certainty in these calculations is due to certain spatiotemporal variations in stand biomass and the impact of environmental factors on vegetation forest biomass increment (Houghton et al. 2001; Turner 2005; Malhi et al. 2006; Ashcroft et al. 2009). Therefore, it is important to explore both aspects to predict how forests are responding to global climate change (Tang et al. 2010; Stegen et al. 2011).

Uncovering the sources of variation in forest biomass is expected to provide baseline information about how spatial interpolation methods may be used to map biomass increments at regional scales. Spatiotemporal variations in stand biomass are affected by both biotic (e.g., forest area, forest age, species composition and planting density) and abiotic (e.g., climate, soil and topography) factors (Potter et al. 2008). Interactions between influencing factors and biomass have been widely reported for tropical zones (Nascimento and Laurance 2001; Baker et al. 2004; Rutishauser et al. 2010; Appendix Table A1). Such influencing factors are primarily climatic (e.g., light, temperature, and precipitation; Hoch and Körner 2008; Zhou et al. 2009), soil (e.g., humus depth, and soil depth; Paoli et al. 2008; Liu et al. 2014), and topographic (e.g., elevation, gradient, and slope position; Castilho et al. 2006; Asner et al. 2009).

However, comprehensive research on biomass and multiple influencing factors is lacking. In the existing research regarding the relationships between topographic, soil, and stand factors, two aspects have been emphasized: the soil factors and the stand factors. However, in-depth research regarding the interactions of all three factors is lacking (Fu et al. 2004). Most studies have only focused on the impacts of a single influencing factor, for example, many studies have demonstrated that elevation is the dominant factor influencing biomass.

Consequently, these studies do not explain the underlying mechanisms of how these factors regulate biomass, and do

not provide a theoretical foundation for sustainable forest management (Baraloto et al. 2011). As a result, many assumptions have been made and many inferences have occurred preventing accurate results. This estimated uncertainty greatly affects the science and reliability of predicting the effects of global climate change (Clark 2002). A lack of knowledge about the factors that influence biomass increment may result in large discrepancies in conclusions drawn about the ecological drivers of spatiotemporal biomass variations and the extent to which they may be extrapolated to construct regional planning maps (Hurt et al. 2010; Zhao et al. 2012). Moreover, because different influencing factors have varying impacts on spatiotemporal variations in biomass, it is important to identify the major influencing factors to provide a theoretical foundation for developing accurate allometric growth models that contain multiple influence-factor variables (Vieilledent et al. 2012).

Combining the Chinese forest management planning inventory (FMPI) and boosted regression tree (BRT) methods provides an effective approach for explaining how multiple influencing factors affect the dynamics of forest biomass (Xi et al. 2008; Ren et al. 2012). In China, the FMPI is used for forest resource planning and design, with the province representing the study unit (Ren et al. 2011).

The FMPI database is updated every 10 years at a regional scale, providing a long-term observational dataset with a large sample size, which may be used to estimate and monitor the availability of wood resources. For example to evaluate the effects of China's afforestation projects on biomass and net primary productivity (NPP), class attribute data (primarily including stand, topographic, and soil factors) from forest management inventories and species-specific biomass regression equations have been applied to surveys of natural forests and plantations (Zhao et al. 2010a, b).

Each patch (forest patch) had a similar area, and vegetation cover and tree volume were determined through system sampling and stratified sampling. The accuracy of the overall stock sampling was 90 % and its reliability 95 % (Lei et al. 2009). Combining GIS with sample survey data to create attribute and spatial data for each forest type represents an effective method for clarifying multi-factor biological impacts of biomass dynamics.

BRT integrates the advantages of two algorithm techniques: specifically, regression trees (models that generate a response to their predictors by recursive binary splits) and boosting (an adaptive method for integrating many simple models to improve predictive performance). BRT models address complex nonlinear relationships and interactions between variables, and are commonly used in ecological studies. Such models have been successfully applied in a range of fields, including ecology (mapping species presence, Moisen et al. 2006, exploring diversity–productivity relations, Zhang et al. 2012) and soil science (mapping

organic carbon, Martin et al. 2011, estimating bulk density, Jalabert et al. 2010).

This study aimed to quantify the relative contributions of the major biotic and abiotic factors on forest biomass increments at a regional scale. We hypothesized that major biotic or abiotic factors could be used to map this increment. As a result, researchers could spatially interpolate forest inventory data to map the biomass increment for environmental factors that are significantly correlated with the increment or variation in a stand factor that explains the increment. If no such correlation exists, spatial interpolation methods in remote sensing could be used to produce maps with this structure without needing to integrate environmental data. Biotic factors, especially stand density, could be derived from remote sensing devices (i.e., radar, Lidar, or optical).

Here, we used the new statistical machine learning technique of BRT to examine how stand, soil, and topographic factors regulate variations in forest biomass increment between 1988 and 2010 in Wuyishan National Nature Reserve (WNNR), China. The screened patches largely represented mature or primary forests with minimal human disturbance. Overall, this study investigated: the spatiotemporal variation of biomass in mid-subtropical forests and the principal factors that influence biomass increment in these forests. Our purpose was to demonstrate the mechanisms involved in achieving biomass increment, and provide baseline information about the practical utility of spatial interpolation methods for mapping forest biomass increments at regional scales.

Materials and methods

Site description

Mid-subtropical forests are the main type in global terrestrial biomes. These forests contain many species with high

biomass and productivity at a regional scale, and are significant for maintaining global carbon balance (Yang et al. 2005). This study was conducted in WNNR. The management authority of this reserve is responsible for the protection of the forest area. No specific permissions were required for the field work at this study location. The field study did not involve endangered, protected, or vertebrate species.

The WNNR (117°27′–117°51′E, 27°33′–27°54′N; Fig. 1) is located in Fujian Province, China. The longest north–south extent of the reserve is 52 km, while the widest east–west extent is 22 km, and its total area is 565.27 km². The WNNR is divided into three functional zones: core, buffer, and experimental. The region's average altitude is 1200 m, while the peak elevation is 2158 m. The average annual temperature is 13.2 °C, and the average annual rainfall is 2368.4 mm. The climate is classified as typical subtropical humid monsoon, and the main soil types include red loam and yellow, yellow–red, and alpine meadow soils.

Major altitudinal variation exists in the study area (800–2158 m), and the topography is complex. There is also major spatiotemporal heterogeneity in forest composition, structure, and biomass. The main tree species include *Castanopsis eyrei*, *Castanopsis carlesii*, *Schima superba*, *Castanopsis fabri*, *Castanopsis sclerophylla*, *Castanopsis tibetana*, *Castanopsis fargesii*, *Quercus fabri*, *Cyclobalanopsis multinervis*, *Pinus taiwanensis*, *Cunninghamia lanceolata*, and *Tsugatche kiangensis*. Though coniferous species (e.g., *P. taiwanensis*, *C. lanceolata*, and *T. kiangensis*) are not characteristic of tropical forests, they are widely distributed in the mid-subtropical forests of China. In the study area, the forest coverage is 96.3 %, with an average planting density of 3208 tree ha⁻¹. The forest community in the study area has a 100-year history of secondary succession.

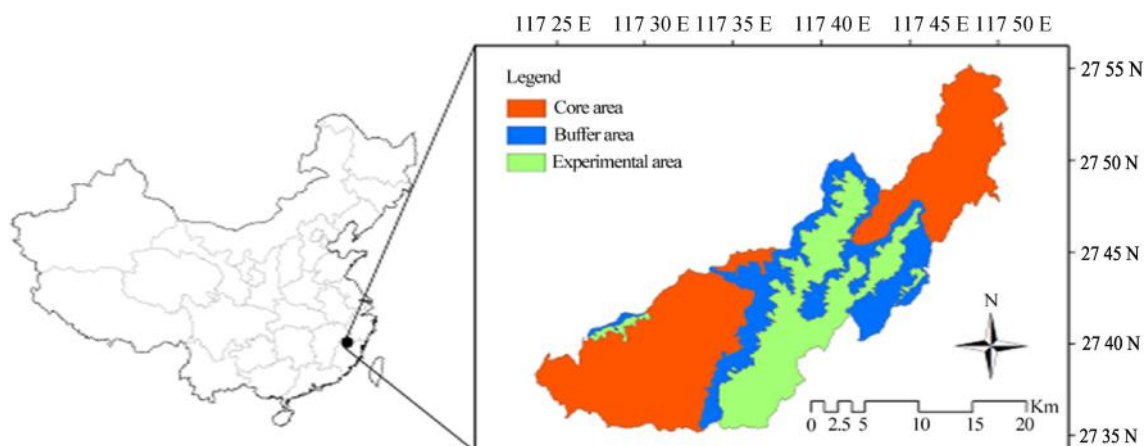


Fig. 1 Geographic location of the Wuyishan National Nature Reserve

Table 1 Statistics of the forest biomass increments (response variable) and the predictor variables

Variables	Names	Units	Min	Max	Mean	SD	<i>n</i>
Response variable							
Forest biomass increment	Biomass increment	t ha ⁻¹	-151.06	154.31	5.96	33.55	2063
Predictor variables							
Initial stand structure							
Species composition	Species	%	0	200	120	30	2063
Forest age	Forest age	a	38	91	64	10.0	2063
Stand density	SD	tree ha ⁻¹	201	2037	481	235	2063
Topography							
Elevation	Elevation	M	340	2042	1068	312	2063
Degree of slope	Degree	°	10	50	31	6	2063
Direction of slope	Direction	a (sunny, <i>n</i> = 186), b (semi-sunny, 881), c (semi-shady, 731), d (shady, 265)					2063
Position of slope	Position	ds (downslope, <i>n</i> = 936), ms (middle slope, 534), us (upslope, 593)					2063
Soil characteristics							
Humus depth	Humus	cm	2	30	11	4	2063
Soil depth	SoilDepth	cm	15	220	61	28	2063
Site index	SiteIndex	I (fertile, <i>n</i> = 270), II (less fertile, 511), III (moderate, 453), IV (infertile, 829)					2063

Min minimum, *Max* maximum, *SD* standard deviation, *n* number of patches

Data sources

The FMPI (10,113 patches) included data from 1988, 2003, and 2010. The FMPI contained stand (species composition, forest age, and stand density), topographic (elevation, degree of slope, direction of slope, and position of slope) and soil (humus depth, soil depth, and site index) attributes, which were averaged for every patch and georeferenced against topographic maps at a scale of 1:10,000. The stand factors were measured for all units within each patch, with the average value being used as the stand factor value for each patch. The overall accuracy of the sampled volumes was checked by measuring difference in the growing stock volumes against those in the estimated field sample plots, based on either systematic sampling, stratified sampling, or cluster sampling.

To estimate the biomass of the Chinese plantation projects and the NPP of the forests, biomass regression models and FMPI data were previously applied to investigate natural and artificial forests (Zhao et al. 2010a, b). These inventories relied on data from a large number of field measurements, and were useful for demonstrating the relationships between the influencing factors and biomass increment in mid-subtropical forests.

Data processing

Sample selection

We screened 2063 out of the 10,113 patches to determine how stand, topographic, and soil factors influence biomass

increment. The WNNR contains core, buffer, and experimental zones, with the patches in the buffer and experimental zones being subject to human disturbance. Patches from buffer and experimental zones, shrublands, plantation forests, bamboo forests and alpine meadows were excluded. We selected patches with only minimal human disturbance from the core zone of the nature reserve, which consisted of arboreal forest. Overall, 11 influencing indicators were detected, including stand, topographic, and soil factors. The indicator values were taken from the FMPI attribute database. Several researchers have found correlations between these indicators and biomass (Nascimento and Laurance 2001; Baker et al. 2004; Rutishauser et al. 2010). Table 1 lists the specific names and statistics of each indicator.

Biomass calculations

Forest biomass was estimated using the viable biomass expansion factor. Parameters for the regression equation were determined by analyzing the relationships between stock volume and biomass using data from different tree species. We focused on subtropical forest biomass. The FMPI data describe each forest patch in the study area in terms of the volume of living trees [diameter at breast height (DBH) >8 cm, tree height >1.3 m]. We estimated forest biomass and determined the parameters of the regression equation from the quantitative relationships between volume and biomass.

Because the environmental conditions and community characteristics are similar to those of subtropical evergreen

Table 2 Values of the parameters for estimating the stand biomass (B , $t\ ha^{-1}$) from the standing volume (V , $m^3\ ha^{-1}$)

Forest types	a	b
<i>Pinus taiwanensis</i>	0.51	1.05
<i>Tsugatche kiangensis</i> , <i>Cryptomeria fortunei</i>	0.40	22.54
<i>Castanopsis eyrei</i> , <i>Castanopsis carlesii</i> , <i>Castanopsis fabri</i> , <i>Castanopsis sclerophylla</i> , <i>Castanopsis tibetana</i> , <i>Castanopsis fargesii</i> , <i>Cyclobalanopsis multinervis</i>	1.04	8.06
<i>Shima superba</i>	0.76	8.31
<i>Quercus fabric</i>	1.33	3.89

The formula is $B = a \cdot V + b$, where parameters a and b are constants for a given forest type that were obtained from Fang et al. (2001)

broadleaved forests, we used the parameters presented by Fang et al. (2001). The forest biomass regression function is represented by $B = a \cdot V + b$, where B is the stand biomass ($t\ ha^{-1}$), V is the standing volume ($m^3\ ha^{-1}$), and a and b are parameters. Dominant species were identified from continuous FMPI data, and we used five groups of parameters to calculate pure forests. For the mixed coniferous, mixed broadleaf and coniferous, and mixed broadleaf forests, we obtained the biomass of specific tree species by using an allocation ratio that was based on tree volume and other parameters specific to the tree species. Next, we summed the biomass estimates of the primary tree species in mixed forests to estimate the total biomass of these forests. Parameter values for different groups of forests are listed in Table 2.

Using a systematic sampling method, the total area of the WNNR was divided into homogeneous patches that covered the entire nature reserve. Therefore, the forest biomass of each patch was calculated as the mean biomass of the patch multiplied by its area. In addition, forest distribution maps representing the biomass over different time periods were generated. In ArcMap, the maps of patches and their attribute information may be queried and used to calculate forest biomass. Spatial analysis using GIS was performed to calculate the spatial distribution of forest biomass increment.

Statistical analysis

We selected the BRT method to examine the factors that regulate biomass increment, and then partitioned the independent influences of these controlling factors. It is an advanced statistical learning method that is based on classification and regression trees, and has several advantages for modeling ecological data (Elith et al. 2008). This method is important and powerful for handling predictor variables of different types (categorical, nominal, and continuous) and distributions (Gaussian, Poisson, binomial, and others), for accommodating missing data and outliers, and for automatically handling interaction effects between predictor variables (De'ath 2007; Elith et al. 2008).

Furthermore, this method has no prior assumptions regarding the independence of predictor variables, is able to fit complex nonlinear relationships, and is highly resistant to the inclusion of large numbers of irrelevant predictor variables.

In the BRT method, multiple trees are fitted and combined in a forward step-wise procedure to predict the response of the dependent variable to multiple predictors (De'ath 2007). Detailed descriptions of BRT modeling are available in Hastie et al. (2009) and in the working guides compiled by Ridgeway (2007) and Elith et al. (2008). Parameter setting is a preliminary step in BRT modeling. Five parameters should be determined: the loss function (for minimizing squared error), learning rate, tree complexity, bagging fraction, and k -fold cross-validation parameters (Ridgeway 2007; Elith et al. 2008; Zhang et al. 2012).

The learning rate is a constant value that is applied to each individual regression tree to determine its contribution to the final model. Tree complexity represents the size of simple regression trees and the maximum depth of variable interactions. With a tree complexity of 1, the model is additive, while the regression tree, which is made of a single-decision stump and two terminal nodes, models the effects of one predictor. With a tree complexity of two or more, each tree accounts for the interactions between two or more input variables. The bagging fraction introduces randomness into a model to reduce overfitting by randomly selecting a portion of the data for model training and validation. The cross-validation value specifies the number of times that the data should be randomly divided for model fitting and validation.

In our study, loss function, bagging fraction, and cross-validation were individually set to Gaussian error structures of 0.5 and 10-fold, as recommended by Ridgeway (2012). The optimal learning rate and tree complexity for achieving the minimum predictive error were determined by using repeated trial-and-error with a combination of settings for the learning rate (0.05, 0.01, 0.005, and 0.001) and tree complexity (1, 2, 3, 4, and 5), as recommended by Ridgeway (2007) and Elith et al. (2008). These optimal

values were selected based on the empirical rules for ecological modeling (Elith et al. 2008). The relative contribution of each predictor variable was estimated by partitioning the total variation explained by each predictor variable (in %). The relationships between the response variables and predictor variables are described by partial dependence patches, which visualize the effects of an individual predictor on the response variable after accounting for the average effects of all of the other variables in the model (De'ath 2007; Elith et al. 2008). The coefficient of determination r^2 and the root mean square error were used to evaluate the model performance. All BRT analyses were conducted in R software (version 2.15.1; R Core Team 2013) using the “gbm” package (Ridgeway 2012).

Results

Spatiotemporal variations of the forest biomass increment

Total biomass increased from 4.62×10^6 t (1988) to 5.30×10^6 t (2010), while the mean biomass density significantly increased from 80.19 ± 0.39 t ha⁻¹ (mean \pm standard error) to 94.33 ± 0.41 t ha⁻¹ (paired t test, $p < 0.001$), with a mean increment rate of 0.64 ± 0.02 t ha⁻¹ a⁻¹. Both forest biomass and biomass increments exhibited very uneven spatial distributions (Fig. 2; Appendix Fig. B1). The mean biomass increment rates decreased significantly with time from 1.46 t ha⁻¹ a⁻¹ (1988–2003) to 0.24 t ha⁻¹ a⁻¹ (2003–2010) (paired t -test, $p < 0.001$). During 1988–2010, the area in which biomass increased was 3.58×10^4 ha, which accounted for 63.6 % of the total area.

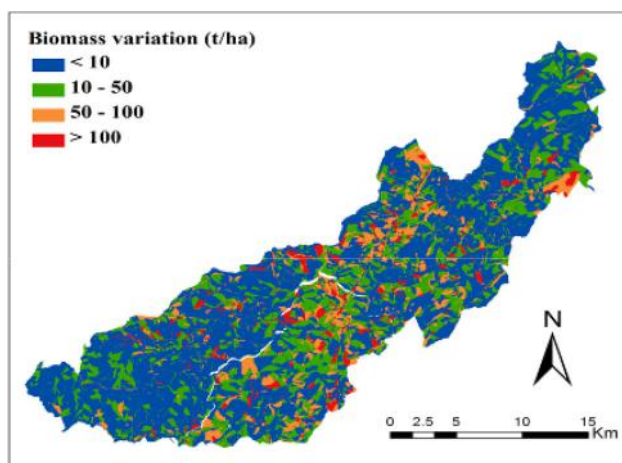


Fig. 2 Spatial distribution of the forest biomass increments between 1988 and 2010

Forest structure change

The natural forest accounted for 95.8 % of the total forest area in 2010 and 99.0 and 96.4 % of the total forest biomass in 1988 and 2010, respectively. The mean biomass increment rates of the coniferous, broadleaf, and coniferous–broadleaf mixed forests were 0.18 ± 0.04 , 0.69 ± 0.04 , and 0.68 ± 0.04 t ha⁻¹ a⁻¹, respectively, and were accompanied by a decrease in stand density (69 ± 22 , 197 ± 27 , and 348 ± 24 tree ha⁻¹ a⁻¹, respectively; Fig. 3).

The area ratio of the coniferous, broadleaved, and coniferous–broadleaved mixed forests changed from 3.0:2.5:4.5 in 1988 to 3.0:3.0:4.0 in 2010. The dominant coniferous species were *P. taiwanensis* and *C. lanceolata*. The forests that were dominated by these two species accounted for 55.8 % of the total coniferous forest area. The mean biomass accumulation rates of the mature coniferous *P. taiwanensis* and *C. lanceolata* forests were 0.22 ± 0.04 , 0.26 ± 0.08 , and 1.22 ± 0.27 t ha⁻¹ a⁻¹, respectively. These accumulation rates were significantly lower (t -test, $p < 0.001$) compared to those obtained for the mature broadleaved forests (dominated by *Ca. carlesii*, *Ca. eyrei*, *Ca. fabri*, *Ca. fargesii*, *Cyclobalanopsis glauca*, *Q. fabri*, and *S. superba*), which exhibited an average accumulation rate of 0.79 ± 0.04 t ha⁻¹ a⁻¹.

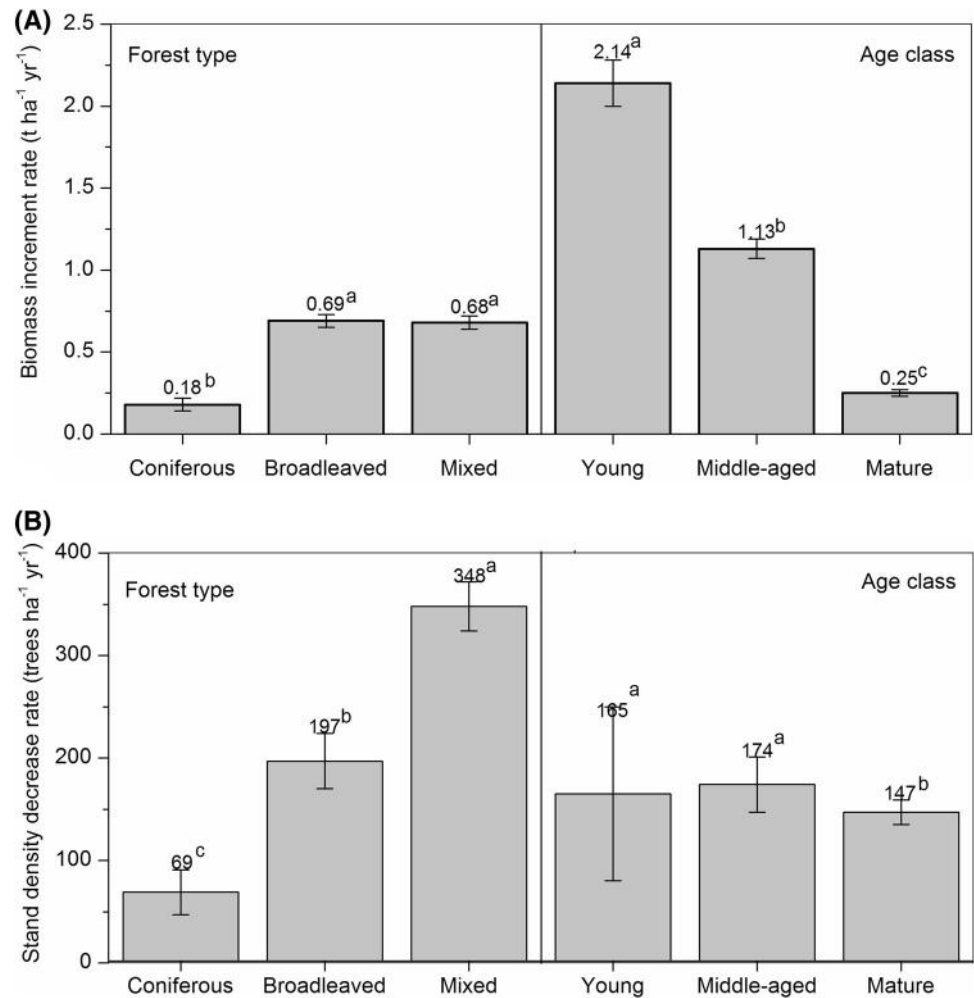
Mean forest age varied between 38 and 91 a, however, most of the age values fell between 51 and 78 a. The effects of age class on the biomass increment rates were significant ($p < 0.001$). The mean biomass increment rates decreased from the young (2.14 ± 0.14 t ha⁻¹ a⁻¹) to intermediate (1.13 ± 0.06 t ha⁻¹ a⁻¹) and mature forests (0.25 ± 0.02 t ha⁻¹ a⁻¹), and was accompanied by a mean annual decrease in stand density (165 ± 85 , 174 ± 27 , and 147 ± 12 trees ha⁻¹ a⁻¹ for all three age classes, respectively; Fig. 3).

Stand and environmental effects on the forest biomass increment

The initial stand, topographic, and soil factors explained 52.9 % of the total variation of the biomass increments from 1988 to 2010. Among these factors, the initial stand factors had the greatest effect on biomass increment (Fig. 4). The relative influence of initial stand factors was (in decreasing order): stand density (34.3 %), species composition (10.2 %), and forest age (9.9 %; Fig. 4). In general, biomass increments increased with increasing age and species composition (Fig. 5).

Elevation was the most important topographic factor (14.7 %; Fig. 4). Biomass generally increased and then decreased with elevation (Fig. 5). The degree of slope only slightly affected biomass increment (7.7 % in relative

Fig. 3 Means of the biomass increment rate (a) and the stand density decrease rate (b) for different forest types within a category. Error bars depict the standard errors. Different letters above the error bars indicate significant differences between the forest types within a category. Bars without a common letter are significantly different ($p < 0.05$)



influence) (Fig. 4). Biomass increased with increasing slope (Fig. 5). The remaining topographic factors (direction and position) had negligible effects (<5.8 % in relative influence) on biomass increment. Biomass tended to increase from exposed (sunny) to sheltered (shaded) slopes and from downslope to upslope regions (Fig. 5).

Soil characteristics only slightly (or negligibly) affected biomass (2.4–9.0 % relative influence) increment (Fig. 4). Biomass increased with increasing site index increased, and fell dramatically at 100–140 cm soil depth (Fig. 5). Biomass decreased in soil humus at <12 cm depth, and increased at moderate soil depths (12–20 cm; Fig. 5).

Discussion

Significance

Various studies have reported spatial variations in forest biomass in relation to stand factors and environmental gradients (Appendix Table A1). Three trends were

observed in these studies: increases in plot area, number of plots, and number of studies involving multiple influence factors (Appendix Table A1). However, few studies have examined temporal variation in forest biomass increment relative to the stand and environmental factors. Therefore, here we focused on biomass increment and analyzed its temporal variation in relation to different stand and environmental characteristics (Chave et al. 2003). The initial stand density and elevation had a stronger influence on total biomass increment variations compared to the other stand and topographic factors. Thus, researchers could apply some variables of forest inventory data (especially stand density and elevation) to map biomass increments (e.g., Alves et al. 2010).

Relative contributions of biomass increment factors

The BRT results indicated that stand factor was the most important influence regulating change in biomass at the landscape scale, whereas topographic and soil factors had less impact. Clark and Clark (2000) and Castilho et al.

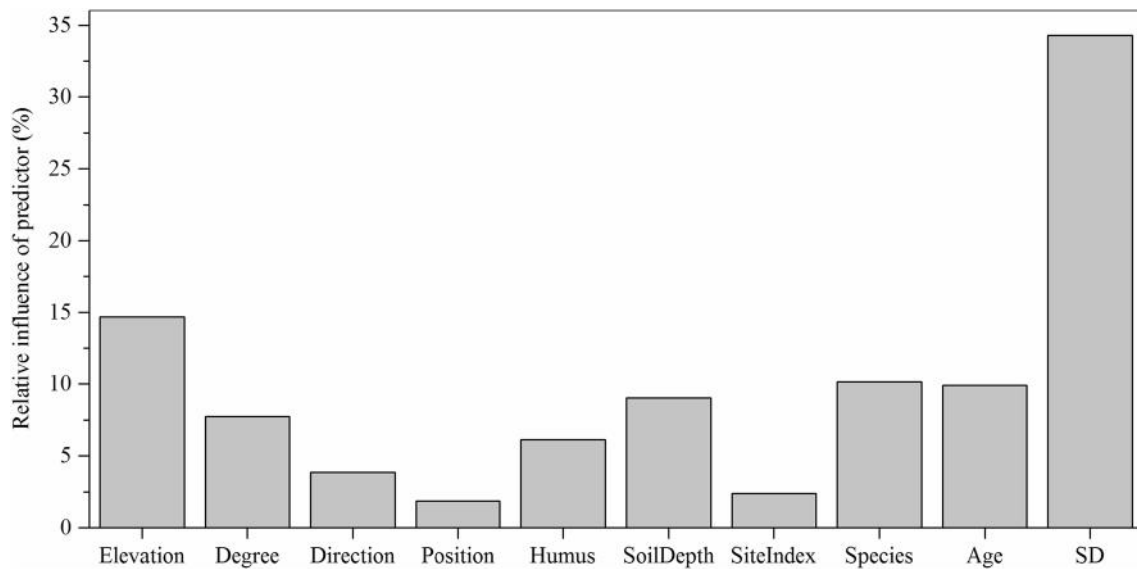


Fig. 4 Results from the boosted regression tree analysis showing the relative influences of the predictor variables on the forest biomass increment (1988–2010). Elevation, Degree, Direction and Position are the topographic factors, Humus, SoilDepth and SiteIndex are the soil

quality variables, and Species, Age and SD are the initial stand structure factors. The relative influence (%) of each predictor variable was calculated by partitioning the total variation explained by each variable. See Table 1 for explanations of predictor variables

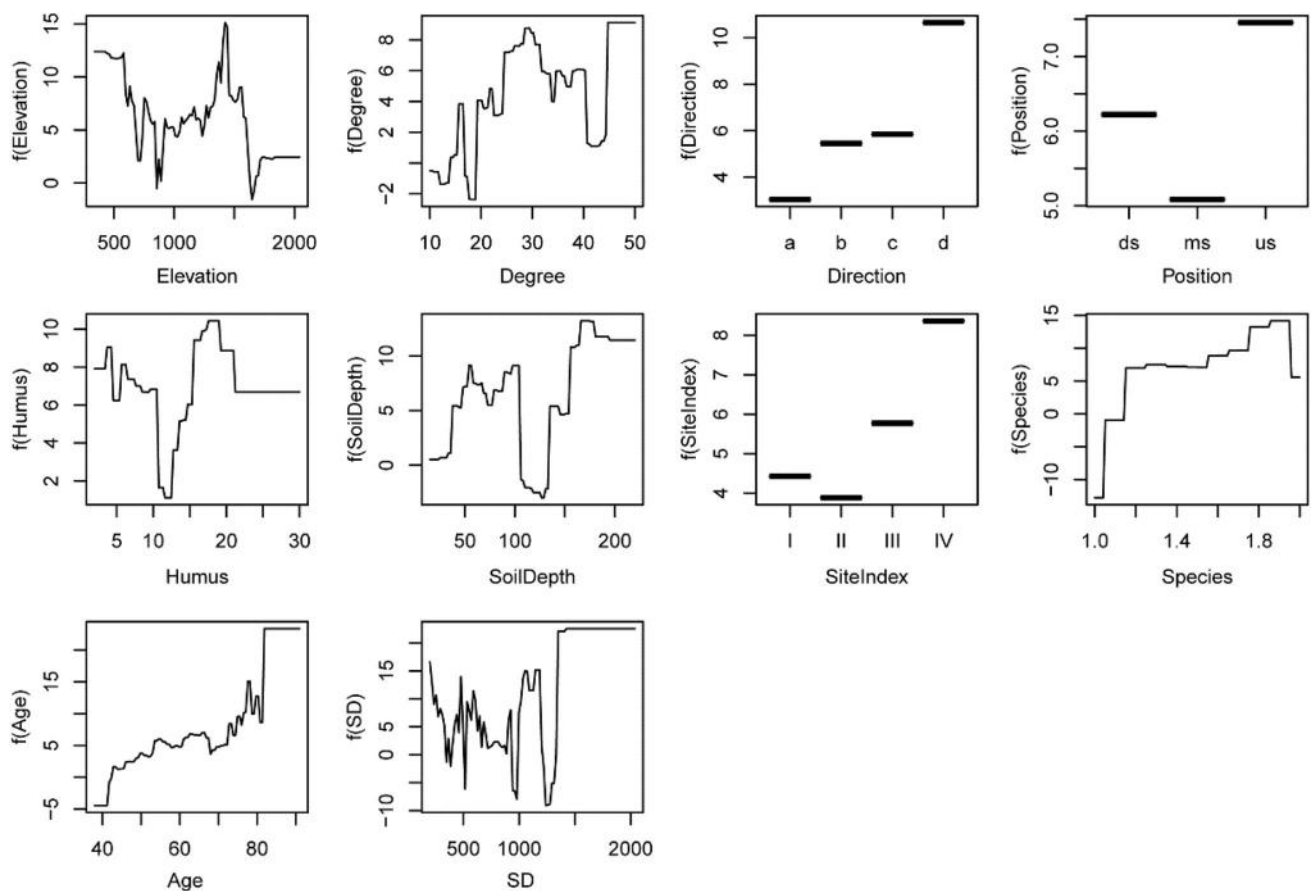


Fig. 5 Partial dependence plots showing the variations in the forest biomass increment (1988–2010) by each predictor variable used in the boosted regression tree model. Elevation, Degree, Direction and

Position are the topographic factors, Humus, SoilDepth and SiteIndex are the soil factors, and Species, Age and SD are the initial stand factors. See Table 1 for explanations of the predictor variables

(2006) also obtained the same results (topographic and soil factors accounted for a third of biomass variation) in their research on rainforest biomass. Compared with static biomass variables, biomass increment has greater dynamic variation. To our knowledge, no previous reports have been published investigating the effects of stand, topographic, and soil factors on biomass increment. However, many studies have emphasized the importance of such research (Baker et al. 2004; Asner et al. 2009; Laumonier et al. 2010; Shao et al. 2011). We believe that our results demonstrate three important parameters influencing forest biomass change.

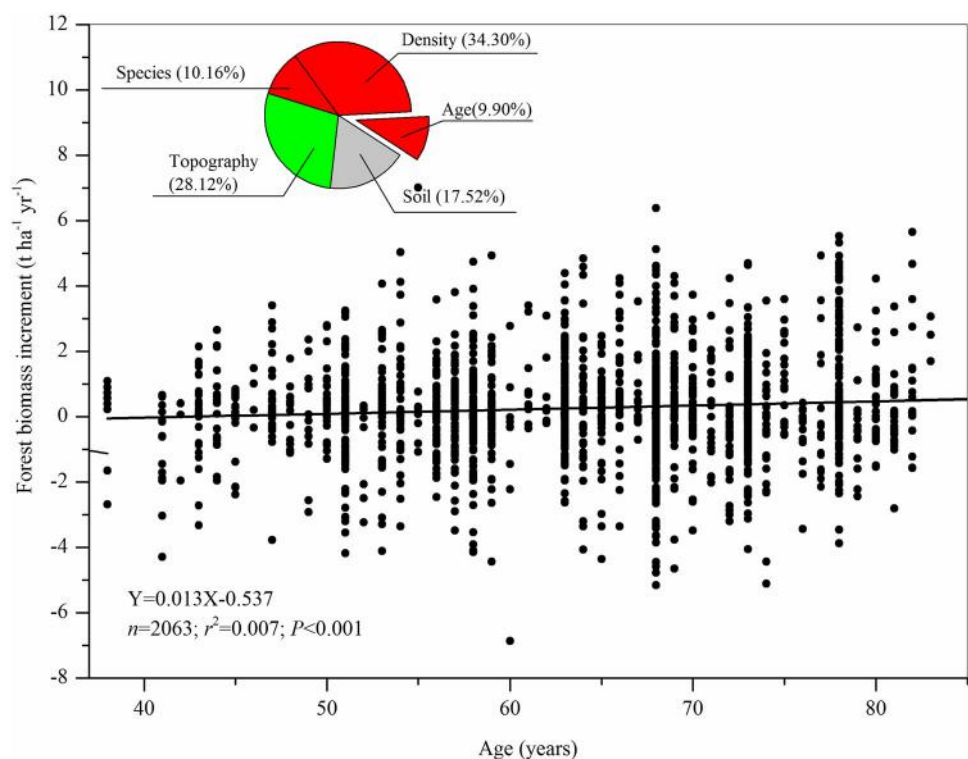
The first element is the scale effect. At smaller spatial scales, Malhi et al. (2006) and Mascaro et al. (2011) demonstrated that the basal area, stand density, and forest age are the primary factors that account for biomass variation. At larger scales, the biomass increment is related to soil nutrient concentrations the soil texture. This relationship occurs because the biomass increment depends primarily on the range of biomass change for large-diameter species (DBH >50 cm) at a small scale. As the spatial scale is expanded, the variability in the biomass increment is influenced by the soil and terrain, which determines the species compositions and physiological limitations of the forest stand. At temporal scales with community succession, during different tree growth (forest age) stages, the dominant influencing factors may vary. Laumonier et al. (2010) found that plots on acidic tuff were the most

distinctive, with fewer and smaller trees, resulting in low biomass.

The second parameter is forest type and associated distribution ranges. Under different growth conditions (e.g., different altitudes), the forest type and composition varies, causing profound changes in forest biomass and its increment (Shao et al. 2011; Ediriweera et al. 2014). For example, Yang et al. (2005) demonstrated that soil texture has a dominant effect on the biomass variation of herbaceous highland meadows. This effect may reduce or increase biomass, primarily depending on its change in direction and size. In addition, because subtropical forests have adequate sunshine and moisture conditions with fertile soils, abiotic factors cannot become ecologically limiting, which is mostly affected by interspecific competition within communities (Asner et al. 2009).

The third parameter is the partitioning of independent influences according to their controlling factors by eliminating the interaction effects. Although researchers have generally acknowledged the indirect relationships between abiotic and stand factors, indirect interactions between terrain and soil factors are rarely expressed quantitatively (Asner et al. 2009). In this study, we selected the BRT method to partition independent influences according to their controlling factors by eliminating the effects of the interactions between the influencing factors. This method has a powerful capacity for automatically handling the interaction effects between predictor variables (De'ath

Fig. 6 Relationships between the forest biomass increments and the forest age. The *inset* shows the relative contributions of the stand (*red*), topography (*green*) and soil (*gray*) factors on the forest biomass increment (1988–2010)



2007; Elith et al. 2008). However, this method cannot provide explicit predictor variable functions.

Of the multiple biological impact factors, our results confirmed that stand density has a dominant effect on biomass increment variability (Fig. 6). This result supports the study by Ma et al. (2012) in the boreal forests of Canada. The authors found that the stand density of vegetation is the most important factor that determines the spatial variability of biomass increment. Stand density directly affects biomass increment through the tree mortality effect and indirectly affects biomass increment by affecting light distribution, soil nutrient distribution, moisture content of the soil, and physiological constraints (Luyssaert et al. 2008). While some studies have suggested that forest age is the most important factor for determining the spatiotemporal distributions of forest biomass (Houghton et al. 2001; Finér et al. 2011), forest age does not necessarily have a dominant effect on biomass increment variability. In particular, most WNNR forests are at the mature stage.

We observed that biomass increment generally increases and then decreases with elevation in the WNNR. In general, biomass has a negative relationship with altitude (e.g., Kitayma and Aiba 2002; Moser et al. 2007; Raich et al. 1997). However, a positive relationship has been observed in relatively moist forests, including forests in tropical (Alves et al. 2010) and temperate zones (Gairola et al. 2011). Although it is difficult to understand all possible causes of a positive biomass–altitude relationship, local topographic variations and nutrient supply are considered important (Alves et al. 2010).

Our patches (located in an area with an altitudinal gradient of 800–1200 m), displayed a positive biomass–altitude relationship that was much smaller than the low-growth limits in subtropical regions. To some extent, local topographic factors (e.g., slope and direction) control plant growth through light, water, and nutrient supplies; thus, indirectly regulating the spatial distribution of biomass. For example, slope regulates the abundance of large trees to some extent. Therefore, more large trees with greater biomass grow on steeper slopes. Below the low-growth limit, a positive relationship between soil moisture and nutrient supply is observed (Alves et al. 2010). Above this limit, nutrient availability for vegetation normally declines with increasing altitude. A lack of soil nitrogen tends to limit plant growth. Thus, it is possible that an increasing-to-decreasing trend of biomass occurs with altitude.

Further study

Because the FMPI data only represent trees with DBH >8 cm, we calculated biomass according to tree height, DBH, and volume data. We did not include the biomass of

shrubs, herbs, ground cover, saplings, seedlings, or dry fallen trees. However, it is important to include understory biomass to obtain accurate biomass estimates (Preece et al. 2012). Moreover, the survey data in this study did not include soil nutrient concentrations (e.g., phosphorus, potassium, and magnesium) or meteorological factors (e.g., temperature, humidity, and solar radiation). Some studies have shown that these indicators also affect the biomass increment at various spatial scales. Therefore, increasing one index may cause the contributions of abiotic factors to biomass to increase (Paoli et al. 2008).

Conclusions

This study provides a technical basis for quantifying the relative contributions of the major influencing factors on forest biomass increment at a regional scale by combining long-term FMPI observations in a BRT model. Our study has strong implications for understanding the factors that explain spatial variation in biomass increment in mid-subtropical forest and for performing spatial interpolation method allocation by predicting the biomass increment. Moreover, this study obtained new knowledge about biotic and abiotic factors involved in biomass increment, which could be used to analyze the mechanisms involved and principal influences on biomass increment in mid-subtropical forests. The results of our analysis showed that total biomass increased from 4.62×10^6 to 5.30×10^6 t between 1988 and 2010, and that mean biomass increased from 80.19 ± 0.39 to 94.33 ± 0.41 t ha⁻¹. At the landscape scale, the stand factor had the greatest influence on forest biomass increment, followed by topographic and soil factors. Soil factors only had slight (or negligible) effects (2.4–9.0 % relative influence). In conclusion, researchers could spatially interpolate forest inventory data to map biomass increment. In addition, more accurate and statistical field sampling protocols should be formulated, primarily with respect to stand (especially stand density) and topographic (especially elevation) factors.

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