The Journal of Animal & Plant Sciences, 30(3): 2020, Page: 730-741
ISSN (print): 1018-7081; ISSN (online): 2309-8694

DIFFERENT CONTRIBUTION OF SPECIES AND FUNCTIONAL TRAIT DIVERSITY TO ABOVEGROUND BIOMASS DYNAMICS IN A FOREST LONG-TERM ECOLOGICAL RESEARCH SITE, SOUTH KOREA

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ABSTRACT

Understanding the key drivers controlling biomass production in forest ecosystems is an important process from both theoretical and practical perspectives. Here, we examined the relationships of aboveground biomass (AGB) production variables with species diversity, community weighted mean (CWM) values and variety of functional traits during temperate forest succession in a forest long-term ecological research site, South Korea. Our results revealed that species diversity and CWM trait values are crucial drivers for AGB production in a Korean temperate forest. The relative importance of the explanatory variables was different among AGB production variables. Mass ratio mechanism by CWM values of dominant traits was a main driver for initial and last AGBs and the increment of AGB by survivors and recruits, whereas AGB loss by mortality of stems was govern by species diversity. The mechanism governing AGB loss associated with species diversity may relate to size-dependent demographic processes of individual woody stems, especially, the withering of canopy trees. Therefore, our results suggest that mass ratio and size-dependent mechanisms of woody plants may be important drivers shaping the AGB dynamics in our study system.

Keywords: Aboveground biomass, Community weighted mean, Long-term ecological research site, Mass ratio mechanism, Size-dependent demographic process, Species diversity.

https://doi.org/10.36899/JAPS.2020.3.0086

INTRODUCTION

During the past few decades, many ecologists and field biologists have implemented ample experimental researches to examine the degree of influence of biodiversity on carbon flux and cycling that affect ecosystem functions and properties (Tilman and Downing, 1994). Vegetation biomass production is a key component of ecosystem functions and processes because the biomass is a main driver for local, regional and global biogeochemical cycles of carbon, water and nutrients (Lohbek *et al*., 2015). To date, most of studies on biodiversity and ecosystem functions and processes have used species diversity such as species richness as a single simple measurement of biodiversity (Cardinale *et al*., 2011). Indeed, the studies have documented the significant relationship between species diversity and biomass productions and changes as proxies of ecosystem functions and processes (Caldeira *et al*., 2005; Con *et al*., 2013; Yuan *et al*., 2016; Li *et al*., 2018). In a plant community, an increase of species diversity can contribute to biomass through niche overlap and complementarity of functionally similar species (Prado-Junior *et al*., 2016). However, the concept of biodiversity includes functional traits and evolutionary history as well as taxonomic diversity (Chun and Lee, 2018). Moreover, species richness alone may be a poor predictor of the functions and processes in natural forest ecosystems (Hooper *et al*., 2005; Zhang *et al*., 2012). In recent, a number of studies have suggested better possibilities of other dimensions of biodiversity such as functional trait diversity (FTD) to assess ecosystem functions and processes (Díaz and Cabido, 2001; Cadotte *et al*., 2011). FTD is defined as the value, variation, distribution and relative abundance of traits of various organisms in ecosystems (Díaz *et al*., 2011). In recent, this FTD-based approach became a promising methodology to understand various ecosystem functions and processes such as carbon and nitrogen cycling and community assembly processes in plant communities (Conti and Díaz, 2013; Bhaskar *et al*., 2014), because FTD enables the quantification of plant life form and characteristics using the same standard and methodology (Poorter *et al*., 2017).

Understanding and analyzing the relationship between plant FTD and aboveground biomass (AGB) is important for the management of carbon storage in AGB and the mitigation of increasing atmospheric carbon dioxide concentration (Díaz *et al*., 2011; Zuo *et al*., 2016). Compared to the relationship of species diversity with AGB, our understanding related to the influence of FTD and the components on AGB in forest ecosystems still remains poor (Ali *et al*., 2017). In general, it is recognized that FTD has two independent components such as community weighted mean (CWM) values and variety of functional trait (VFT). CWM represents the degree dominated by a single strategy in a community and refers to the mass ratio hypothesis (Grim, 1998; Bhaskar *et al*., 2014). And under this hypothesis, plant communities dominated by species with a single strategy of resource use have high biomass. Unlike CWM, VFT indicates the variation and/or range of trait values within single or multiple functional spaces in a community and relates to niche complementarity theory (Tilman, 1997; Petchey and Gaston, 2006). Under niche complementarity theory, a variety of species or functional traits can drive niche partitioning with the use of different resources by coexisting species, thus plant communities involving diverse species with a high species diversity or VFT have higher biomass (Ali *et al*., 2017). Although these two components of FTD and species diversity explain different mechanisms, both hypotheses are not mutually exclusive and can be jointly control biomass dynamics as key components of ecosystem functions and processes (Prado-Junior *et al*., 2016).

Moreover, previous studies on these subjects in forests showed different relationships between biodiversity (especially, species diversity) indices and aboveground biomass at different spatial scales (Zhang *et al*., 2012). Chisholm *et al*. (2013) found that relationships between species diversity and aboveground biomass at small spatial scales may be attributable to local variation in woody species density and niche complementarity, while the effects at large spatial scales may be associated with environmental variables. However, these researches on the effect of spatial scale are limited to species diversity but not functional diversity (Ali *et al*., 2017).

In these contexts, we explored the production and change of AGB for 1 ha permanent plot at a long-term ecological research (LTER) site in South Korea. For standing individuals of woody plants, we calculated nine diversity indices (i.e., two species diversity indices and seven FTD indices) and four variables relevant to AGB dynamics at two different spatial scales. We examined 1) how species diversity and FTD are associated with AGB dynamics in a natural forest ecosystem, 3) whether the effects of these two main diversity indices (i.e., species diversity vs. FTD) on AGB dynamics are independent or not, and finally 3) whether the mass ratio (measured by CWM) or niche complementarity (measured by VFT) mechanisms drive variations in AGB dynamics for 20 years forest monitoring and which mechanism has dominant effect in this study area.

MATERIALS AND METHODS

Study area: The present study was implemented in a 1-ha (100 m × 100 m) permanent plot of a LTER site located in Mt. Gyebang that is a representative cool temperate forest, South Korea (Fig. 1). Mt. Gyebang belongs to a temperate deciduous and coniferous mixed forest biome and a mountain ecoregion and the bedrock consists of granite gneiss (Chun *et al*., 2014). The mean annual temperature and precipitation of the LTER site are approximately 9.2°C and 1268 mm (Chun *et al*., 2014). The dominant woody plant species in the site are *Acer pseudosieboldianum* (Pax) Kom., *Betula schmidtii* Regel, *Magnolia sieboldii* K. Koch, *Pinus densiflora* Siebold & Zucc., *Quercus mongolica* Fisch. ex Ledeb. and *Tilia amurensis* Rupr..The permanent plot in the site was established and managed by the National Institute of Forest Science since starting survey from 1997. The plot has regularly investigated the changes of biodiversity, nutrient cycling, vegetation structure and dynamics by various research groups in South Korea (Chun *et al*., 2014). The permanent plot was divided and marked into 100 quadrats (10 m × 10 m) in the field and surveyed over 20 years. Field survey of woody plants were implemented every five years and all standing stems of woody species ≥ 2cm diameter at breast height (DBH) were identified, tagged and measured for DBH and height with a standard LTER survey protocol from National Institute of Forest Science (Lim *et al*., 2003; Chun *et al*., 2014; Chun and Lee, 2019). In this study, we divided the data of 1-ha plot in the LTER site into non-overlapping 100 10 m × 10 m quadrat data and 25 20 m × 20 m quadrat data. Therefore, we implemented all analyses with these two spatial scale data in this study.

Plant functional traits and calculation of species and functional trait diversity: To test the relationship between species diversity and AGB production variables, we used two indices of species diversity such as species richness and Shannon H. Species richness was defined as the number of species in each quadrat. Shannon H was calculated in each quadrat as follows;

$$\text{Shannon H} = -\sum_{i-1}^{n} p_i \ln p_i$$

where n and p_i are the number of species and the relative abundance of the ith species in each quadrat, respectively.

To test the relationship between FTD and AGB production variables, we used three functional traits associated with ecosystem functioning and process such as maximum height (MH; *m*), leaf size (LS; *cm*) defined as the sum of leaf length and width and wood density (WD; g/cm^3). MH is a major factor affecting plant access to light and the important axis of life history and longevity (Chun and Lee, 2018). LS is important in terms of water balance and leaf energy (Chun and Lee, 2019). Lastly, WD is the key factor related to a trade-off between tree growth rate and defenses against physical damage by biotic and abiotic factors (Chun and Lee, 2019). The plant traits in this study were obtained from open accessible databases and published literature (Appendix 1). We used mean trait values for each woody plant species to quantify functional trait diversity, thus, the evaluation of trait variation within a species was impossible in this study. Moreover, to explore the degree of associations between FTD and AGB production variables, two different types of FTD were calculated, namely the dominant trait values (Garnier *et al*., 2004) and the variety of trait values (Mason *et al*., 2003) expressed by community weighted mean (CWM) and functional divergence (FD), respectively. CWM and FD values of a single trait were calculated in each quadrat. CWM represents the mean trait value for unit AGB in a quadrat, whereas FD indicates dispersion of each trait apart from mean value (Conti and Díaz, 2013). The CWM and FD were quantified for each trait x in each quadrat as follows;

$$\mathrm{CWM}_x = \sum_{i-1}^{n} p_i\, t_i$$

$$\mathrm{FD}_x = {}^{2}/_{\pi}\arctan(5\mathrm{V}) \text{ and } \mathrm{V} = \sum_{i-1}^{n} p_i(\ln t_i - \ln t)^2$$

where, p_i and t_i represent the relative abundance and the trait value of ith species in a quadrat, respectively. And $\ln t = \sum_{i=1}^{n} p_i \ln t_i$. The value of FD ranges between 0 and 1. We also measured the variety of multiple functional traits using multifunctional divergence index, $\mathrm{FD}_{\mathrm{MT}}$, which calculates the distance among species weighted by their abundance from the center of a multi-functional trait space (Conti and Díaz, 2013). We used *functcomp*, *dbFD* and *vegan FD* package in R version 3.4.4 to quantify the values of CWM and FD (Finegan *et al*., 2015; Zuo *et al*., 2016). Descriptive statistics of all the species and functional diversity indices at two spatial scales are provided in Fig. 2.

Quantification of aboveground biomass productions: AGB for each individual ≥ 2 cm DBH in the plot was estimated using allometric equations with stem DBH as the predictive variable (Table 1). The data from the first and last monitoring were used to quantify AGB production variables. With the AGB at individual level, the four variables of AGB production were calculated at two spatial quadrat levels such as 10×10 m^2 and 20×20 m^2: 1) total annual increment of AGB by survivors and recruits ($\Delta\mathrm{AGB}_{\mathrm{tinc}}$; Mg ha^{-1} year^{-1}), that is, $\Delta\mathrm{AGB}_{\mathrm{tinc}}$ is the sum of annual growth in ABG of individuals that were survived between the first and last monitoring and annual increment of AGB by recruitment into minimum DBH (≥ 2 cm) between the two monitoring, 2) annual loss of AGB due to dead individuals between the first and last monitoring ($\Delta\mathrm{AGB}_{\mathrm{loss}}$; Mg ha^{-1} year^{-1}), 3) initial AGB at the first monitoring ($\mathrm{AGB}_{\mathrm{init}}$; Mg ha^{-1}) and 4) last AGB at the last monitoring ($\mathrm{AGB}_{\mathrm{last}}$; Mg ha^{-1}). Summary statistics of AGB production variables at two spatial scales are shown in Fig. 2.

Statistical analysis: Simple ordinary least squares (OLS) regression model was conducted to test the bivariate relationship of four AGB production variables with two species diversity (i.e., species richness and Shannon H) and seven functional trait diversity (i.e., three CWMs and four FDs) indices. We also performed multiple OLS regression models with all possible combinations of species (i.e., multi-model inference) and functional trait diversity indices on each AGB production variable. Only significant indices for each AGB production variables were used in multiple OLS regression models to select the best models. We selected the best models that had the lowest corrected Akaike information criterion ($\mathrm{AIC}_{\mathrm{c}}$) value (Prado-Junior *et al*., 2016). If the differences in AIC between selected models were less than 2 (i.e, $\Delta\mathrm{AIC}_{\mathrm{c}} < 2$), the models were regarded to have equivalent support (Prado-Junior *et al*., 2016). And in the case of nearly equivalent support for selected models, we selected the most parsimonious model with the lowest number of explanatory variables. We assessed the relative importance of each diversity indices by comparing the standardized regression coefficients of diversity indices for each AGB production variable in the best model. All statistical analyses were performed with SAM version 4.0 and PAST version 2.17.

RESULTS

From bivariate analysis at a spatial scale of 10×10 m^2 (Table 2), $\Delta\mathrm{AGB}_{\mathrm{tinc}}$ was positively related to $\mathrm{CWM}_{\mathrm{MH}}$ and $\mathrm{CWM}_{\mathrm{WD}}$, whereas at a spatial scale of 20×20 m^2, it was negatively correlated with $\mathrm{CWM}_{\mathrm{LS}}$ but has positive correlation with $\mathrm{CWM}_{\mathrm{WD}}$. $\Delta\mathrm{AGB}_{\mathrm{loss}}$ was negatively correlated only with Shannon H at 10×10 m^2 spatial scale whereas it was negatively correlated with species richness, Shannon H and $\mathrm{FD}_{\mathrm{MH}}$. At both spatial scales, $\mathrm{AGB}_{\mathrm{init}}$ and $\mathrm{AGB}_{\mathrm{last}}$ had positive relationships with $\mathrm{CWM}_{\mathrm{MH}}$ and $\mathrm{CWM}_{\mathrm{WD}}$ and $\mathrm{AGB}_{\mathrm{init}}$ had negative correlation with $\mathrm{FD}_{\mathrm{MH}}$. And two indices of species diversity were negatively correlated with $\mathrm{AGB}_{\mathrm{init}}$ at both spatial scales and $\mathrm{CWM}_{\mathrm{LS}}$ was negatively correlated only with $\mathrm{AGB}_{\mathrm{last}}$ at 20×20 m^2 spatial scale. The results from multi-model inference were similar to those of simple OLS. That is, mainly CWM-related FTD indices were more important variables to predict $\Delta\mathrm{AGB}_{\mathrm{tinc}}$, $\mathrm{AGB}_{\mathrm{init}}$ and $\mathrm{AGB}_{\mathrm{last}}$ and species diversity indices were crucial predictors for $\Delta\mathrm{AGB}_{\mathrm{loss}}$. Furthermore, the standardized regression coefficient of each significant diversity index also reinforced the results of simple and multiple regression models (Fig. 3). Species diversity indices for $\Delta\mathrm{AGB}_{\mathrm{loss}}$ were the most important predictors whereas the effect of CWM indices for the other three AGB production variables (i.e., $\Delta\mathrm{AGB}_{\mathrm{tinc}}$, $\mathrm{AGB}_{\mathrm{init}}$ and $\mathrm{AGB}_{\mathrm{last}}$)

were higher than those of species diversity and FD indices.

Table 1. Allometric equations for the estimation of aboveground biomass (AGB) for woody plant species used in this study. DBH indicates diameter at breast height.

Species	Equation	Reference
Abies holophylla	$AGB = 0.0647 \times DBH^{2.608}$	Kwak *et al*. (2004)
Acer manschuricum	$AGB = 0.0335 \times DBH^{1.606} + 0.0026 \times DBH^{3.323} + 0.1222 \times DBH^{2.310}$	He *et al*. (2018)
Acer pictum	$AGB = 0.017 \times DBH^{1.948} + 0.008 \times DBH^{2.934} + 0.075 \times DBH^{2.408}$	Wang (2006)
Carpinus laxiflora	$AGB = 0.255 \times DBH^{2.001} + 0.005 \times DBH^{3.167} + 0.000007 \times DBH^{4.413}$	Son *et al*. (2014)
Juglans mandshurica	$AGB = 0.0156 \times DBH^{1.974} + 0.0041 \times DBH^{3.063} + 0.0861 \times DBH^{2.381}$	He *et al*. (2018)
Pinus densiflora	$AGB = 0.235 \times DBH^{2.071} + 0.004 \times DBH^{2.748} + 0.054 \times DBH^{1.561}$	Son *et al*. (2014)
Pinus koraiensis	$AGB = 0.064 \times DBH^{2.377} + 0.621 \times DBH^{1.395} + 0.025 \times DBH^{2.237}$	Son *et al*. (2014)
Populus tremula var. *davidiana*	$AGB = 0.00166 \times DBH^{2.5495} + 0.001140 \times DBH^{3.2079} + 0.10732 \times DBH^{2.3450}$	Dong *et al*. (2015)
Quercus mongolica	$AGB = 0.595 \times DBH^{1.766} + 0.007 \times DBH^{2.970} + 0.005 \times DBH^{2.362}$	Son *et al*. (2014)
Tilia amurensis	$AGB = 0.0027 \times DBH^{2.368} + 0.0021 \times DBH^{3.131} + 0.0965 \times DBH^{2.323}$	He *et al*. (2018)
Ulmus davidiana var. *japonica*	$AGB = 0.0044 \times DBH^{2.438} + 0.0068 \times DBH^{3.001} + 0.1308 \times DBH^{2.271}$	He *et al*. (2018)
Other broadleaved species	$AGB = 0.1673 \times DBH^{2.393}$	Lim *et al*. (2003)
Other coniferous species	$AGB = 0.086 \times DBH^{2.393}$	Lim *et al*. (2003)

Table 2. Relationships between aboveground biomass (AGB) and diversity indices using simple ordinary least squares regression models in the study site of Mt. Gyebang, South Korea.

Spatial scale	Variable	ΔAGB_{tinc}		ΔAGB_{loss}		AGB_{init}		AGB_{last}	
		t	R^2	t	R^2	T	R^2	t	R^2
10 m × 10 m	Species diversity								
	Species richness	–0.041	<0.001	–1.940	0.037	–2.305	0.051^{*}	–0.735	0.005
	Shannon H	–0.061	<0.001	–2.183	0.046^{*}	–2.366	0.054^{*}	–0.686	0.005
	Community weighted trait mean (CWM)								
	CWM_{MH}	3.325	0.101^{***}	1.556	0.024	6.206	0.282^{***}	5.780	0.254^{***}
	CWM_{LS}	–0.777	0.006	0.782	0.006	–0.709	0.005	–1.402	0.020
	CWM_{WD}	2.755	0.072^{**}	0.896	0.008	4.878	0.195^{***}	4.516	0.172^{***}
	Functional divergence (FD)								
	FD_{MH}	–0.501	0.003	–1.507	0.023	–2.950	0.082^{**}	–1.572	0.025
	FD_{LS}	–0.042	<0.001	–0.412	0.002	–1.865	0.034	–0.738	0.006
	FD_{WD}	–1.379	0.019	1.485	0.022	1.721	0.029	0.801	0.007
	FD_{MT}	1.232	0.015	1.617	0.026	2.191	0.047^{*}	0.675	0.005
20 m × 20 m	Species diversity								
	Species richness	–0.838	0.030	–2.550	0.22^{*}	–3.145	0.301^{**}	–1.334	0.072
	Shannon H	–1.586	0.099	–2.093	0.16^{*}	–3.230	0.312^{**}	–1.875	0.133
	Community weighted trait mean (CWM)								
	CWM_{MH}	1.995	0.147	1.924	0.139	6.231	0.628^{***}	3.658	0.368^{***}
	CWM_{LS}	–2.277	0.184^{*}	0.075	<0.001	–1.945	0.141	–2.479	0.211^{*}
	CWM_{WD}	2.080	0.158^{*}	0.914	0.035	4.209	0.435^{***}	3.372	0.331^{**}
	Functional divergence (FD)								
	FD_{MH}	–1.288	0.067	–2.096	0.16^{*}	–4.312	0.447^{***}	–2.177	0.171^{*}
	FD_{LS}	0.060	<0.001	–0.475	0.01	–0.346	0.005	0.097	<0.001
	FD_{WD}	–1.155	0.055	1.838	0.128	0.476	0.010	–1.102	0.050
	FD_{MT}	–0.423	0.008	0.011	<0.001	–0.527	0.012	–0.562	0.014

Note: The abbreviations for all predictors and response variables are defined in Figure2. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 3. Best models and the regression coefficients of selected predictors obtained from a series of multiple regression analyses for four biomass components and 9 predictors using multi-model inference.

Variable	ΔAGB_{tinc}		ΔAGB_{loss}		AGB_{init}		AGB_{last}	
	10 × 10 m^2	20 × 20 m^2	10 × 10 m^2	20 × 20 m^2	10 × 10 m^2	20 × 20 m^2	10 × 10 m^2	20 × 20 m^2
Constant	–3.281	5.899	5.382	5.192	–2.961	–1.635	–3.461	6.245
Species diversity								
Species richness				–0.3				
Shannon H			–2.353		–0.824	–3.264		
Community weighted mean (CWM)								
CWM_{MH}	0.179				0.159	0.656	0.129	
CWM_{LS}		–0.494						–1.208
CWM_{WD}	6.53	11.349			3.609		5.123	39.657
Functional divergence (FD)								
FD_{MH}					1.008			
FD_{LS}								
FD_{WD}								
FD_{MT}								
Model								
R^2	0.121^{**}	0.309^{*}	0.046^{*}	0.22^{*}	0.386^{***}	0.730^{***}	0.254^{***}	0.496^{***}
AIC_c	454.162	83.945	506.158	94.25	237.258	91.695	304.161	118.442

Note: The coefficient of determination (R^2) and Akaike Information Criterion (AIC_c) of the best models are given. The abbreviations for all predictors and response variables are defined in Figure2.* $P< 0.05$; ** $P< 0.01$; *** $P< 0.001$.

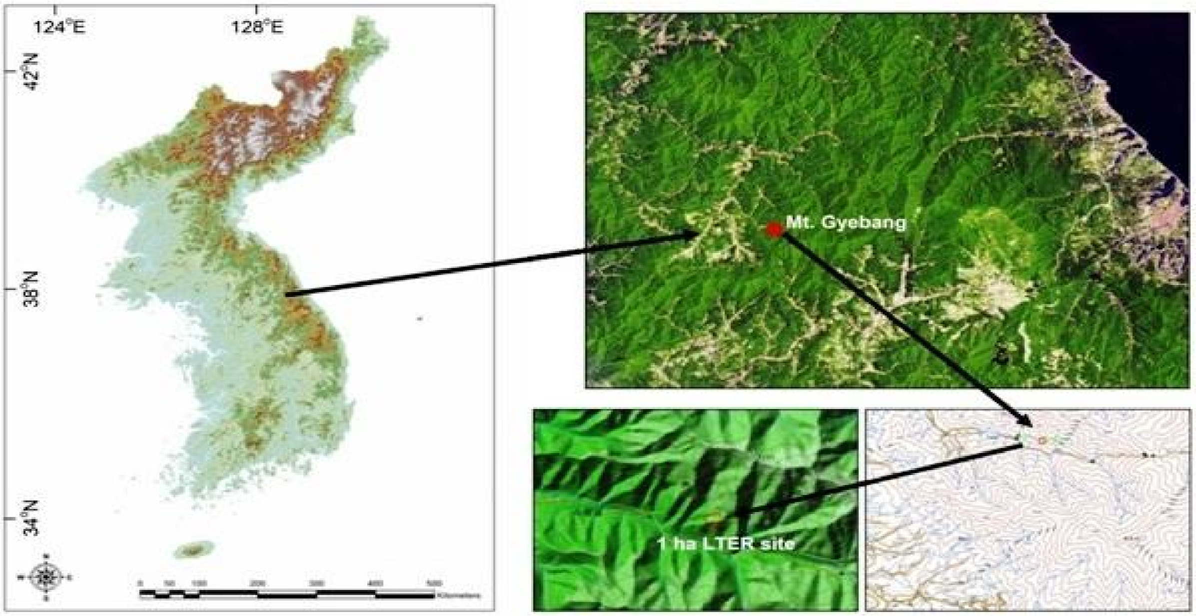

Figure 1. Location of the study area, 1 ha long term ecological research (LTER) site, in Mt. Gyebang, South Korea.

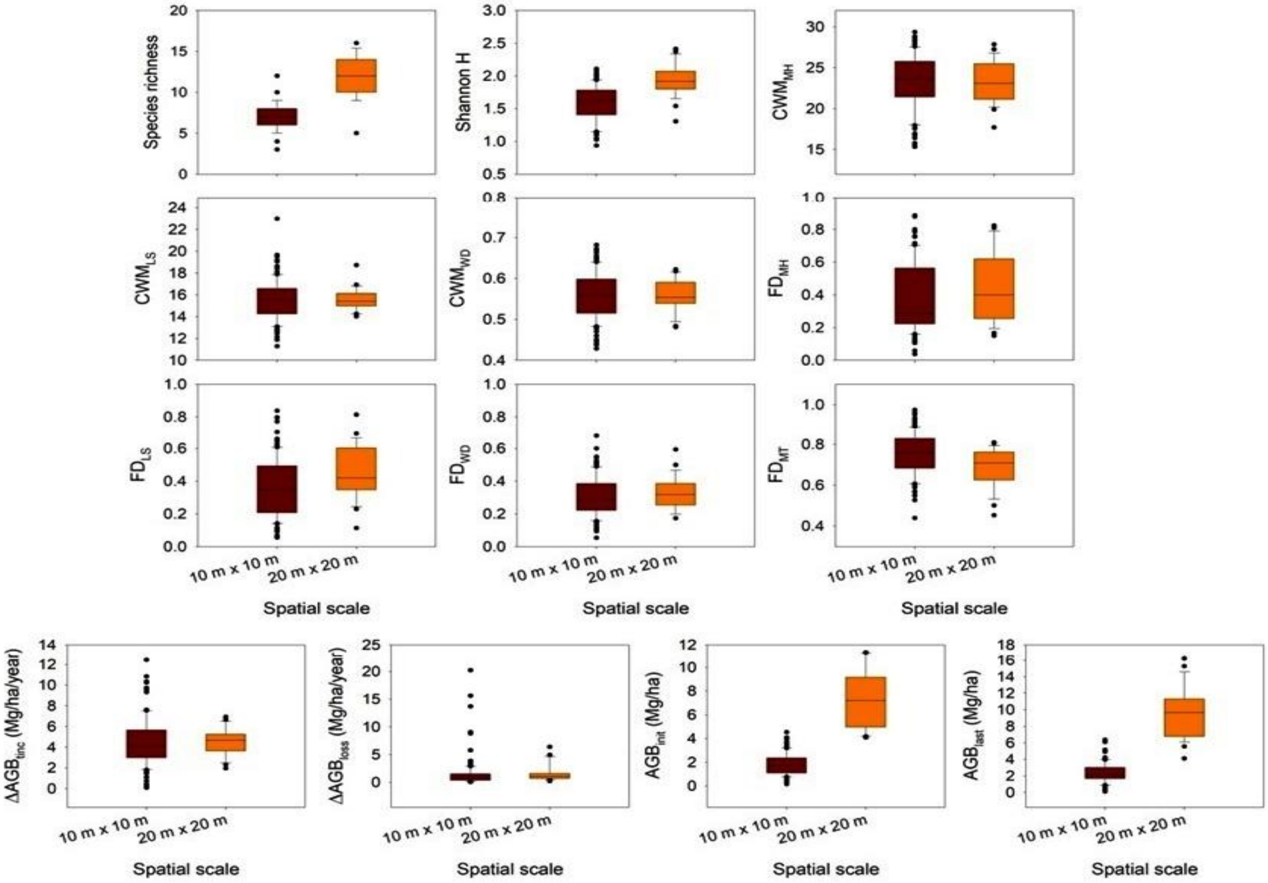

Figure 2. Descriptive statistics of all predictors and response variables at two spatial scales in a LTER site of Mt. Gyebang, South Korea. Note: AGB, aboveground biomass; ΔAGB_{tinc}, total annual AGB increment; ΔAGB_{loss}, annual AGB loss due to mortality; AGB_{init}, initial AGB at the first census; AGB_{last}, AGB at the last census; CWM, community weighted mean; FD, functional divergence; MH, maximum height; LS, leaf size; WD, wood density; MT, multiple traits.

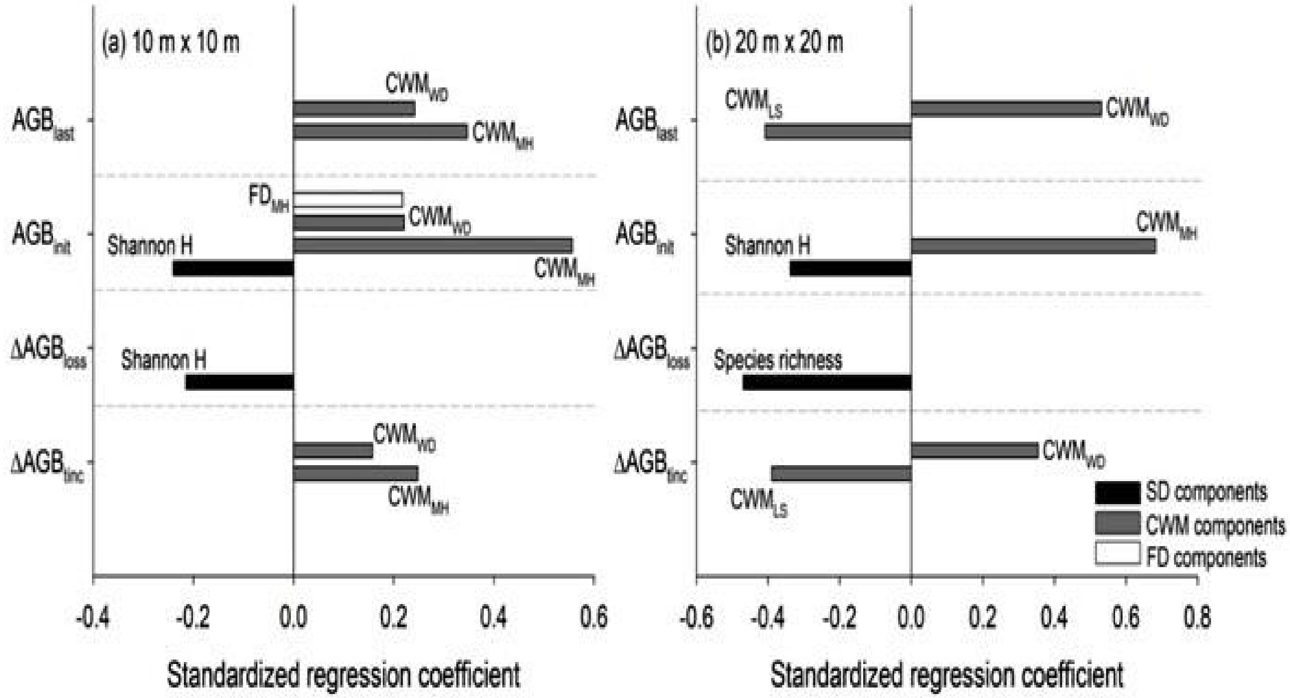

Figure 3. Comparison among the effects of species diversity (SD), community weighted mean (CWM) and functional divergence (FD) on the four aboveground biomass (AGB) in a LTER site of Mt. Gyebang, South Korea.

Note: Standardized coefficients can directly be compared among the components of SD, CWM and FD; the higher value, the stronger the relationship observed. The variables selected from the best models were included (please see Table 3 for more information). The abbreviations for all predictors and response variables are defined in Figure2.

DISCUSSION

The present study explored the direct relationships between AGB production variables and two different components of biodiversity (i.e., species vs. functional diversity) in a temperate forest ecosystem using 20-years forest succession data from a LTER site in South Korea. We found that AGB production variables were related to CWM-related and species diversity-related predictors although FD_{MH} is significantly correlated with AGB_{init} in simple OLS models. Especially, CWM values of functional traits (i.e., maximum height, leaf size and wood density) had significant relationships with ΔAGB_{tinc}, AGB_{init} and AGB_{last}. And species diversity had negative correlations with annual AGB loss due to mortality (i.e., ΔAGB_{loss}).

When considering only two components of FTD except for species diversity components, our results indicate that relative importance and contribution of two components of FTD are different and also suggest that mass ratio mechanism dominate AGB dynamics rather than niche complementarity mechanism in our study site. Recent studies have also suggested mass ratio hypothesis is superior to niche complementarity hypothesis in shaping the patterns of AGB stocks and dynamics in forest ecosystems (Conti and Díaz, 2013; Finegan *et al*., 2015). Most studies on FTD and AGB dynamics assume that the relationships between the both variables are similar in both species and community levels. Thus, they supposed that acquisitive traits (e.g., high leaf size, low wood density) dominant communities will lead to fast AGB growth, whereas conservative traits (e.g., high wood density) dominant communities will have large AGB. Moreover, the maximum adult height of a woody species reflects the adult status for survival and growth and is positively correlated with AGB productions through functional dominant strategy (Finegan *et al*., 2015; Prado-Junior *et al*., 2016). Actually, we found that CWM values of wood density are related to the increase of AGB stocks (i.e., AGB_{init} and AGB_{last}), either directly because high wood density represents more AGB per wood stem volume, or indirectly because wood density enhances the longevity of individual stems (Bennett *et al*., 2015; Poorter *et al*., 2017). Other studies also revealed that wood density has strong positive effect on AGB stocks (Barrufol *et al*., 2013; Poorter *et al.,* 2017).

In the present study, higher CWM values of maximum adult height were associated with higher annual AGB increment by survivors and recruits as well as AGB stocks. In general, maximum height is recognized as one of the major axes of plant functional traits for light competition and capture in forest ecosystems (Kitajima and Poorter, 2010). Our results are consistent with other earlier studies (Poorter *et al*., 2008; Wright *et al*., 2010; Finegan *et al*., 2015; Zuo *et al*., 2016), which revealed that communities with a high percent AGB of potentially tall plant species tended to have high AGB productions. Thus, our study supports that the potential important of the stature of mature woody plants for survival and growth in closed and tall canopy systems and also for ecosystem functions and processes (Poorter *et al*., 2006; Wright *et al*., 2010; Finegan *et al*., 2015). Moreover, CWM values of leaf size were negatively correlated with annual AGB increment only at 20 × 20 m^2 spatial scale (Tables 2 and 3) despite of CWM values of maximum height as the best predictor at 10 × 10 m^2. Leaf size is a trait associated with acquisitive resource strategies (Pacala and Rees, 1998). When resources are abundant (e.g., early succession stage), species with acquisitive resource-use traits (e.g., low wood density, high leaf size) are dominant because the species grow and reproduce faster (Pacala and Rees, 1998). However, as resource become deficient (e.g., late succession stage), species with conservative resource-use traits (e.g., high wood density and seed mass) increase and acquisitive species decrease (Chazdon, 2008). Therefore, our study from these relationships between CWMs and AGB production variables suggests the study site is mainly dominated by potentially tall conservative species with high wood density. Furthermore, the results also indicate the main dominant trait to drive change in AGB production may be different between spatial scales.

Unlike other AGB production variables, annual AGB loss due to stem mortality were negatively correlated with species diversity indices such as species richness and Shannon H. Previous studies hypothesize that high species diversity affect AGB productions through various mechanisms such as competitive exclusion, facilitation and insurance effect (Poorter *et al*., 2006; Barrufol *et al*., 2013; Poorter *et al*., 2017). And they found species diversity enhance the overall AGB stocks and lead to larger AGB dynamics but also to higher AGB loss due to mortality. However, in our study, higher species diversity led to lower AGB loss which is inconsistent with the results of other previous study. These results in our study can be explained by few large stems or many small stems in quadrats. That is, if a quadrat occupied by a large tree with high AGB had low species diversity, when the large tree was withered, the quadrat will undergo high AGB loss. On the other hand, if there were many seedling or sapling of various species in quadrats with a large gap formed after withering of a large tree, the quadrats will show lower AGB loss despite of withering of the same number of stems when compared with the former case. Indeed, Chun *et al*. (2014) reported that the mortality of stems of same number but different size lead to different AGB loss among quadrats in this LETR site. Therefore, our study suggests that the importance of species diversity on annual AGB loss may be different depending on existence of forest gaps and canopy trees at least in our study system.

In this study, we also found that AGB production variables generally were related to more biodiversity indices at small spatial scale (i.e., 10 × 10 m^2) than large spatial scale (i.e., 20 × 20 m^2). Chisholm *et al*. (2013) reported this scale-dependent results are associated with theoretical models that niche complementarity and sampling effects are involved at small scales, whereas environmental variables also control the relationships at larger scales. Although we did not consider environmental variables in this study, our results also indicated that niche complementarity and sampling effects contributed more to AGB production variables (Fig. 3). In our results on scale-dependent relationships of FTD and species diversity to AGB production variables, we suggest that models be developed to combine large-scale environmental variables with small-scale related factors (Chisholm *et al*., 2013)

Conclusions: Understanding the key drivers controlling biomass stocks and dynamics in forest ecosystems is a meaningful process from both theoretical and practical perspectives (Conti and Díaz, 2013; Poorter *et al*., 2017). The present study indicates that species diversity and community weighted mean trait values are crucial drivers for aboveground biomass productions in a Korean temperate forest. However, the relative importance and contribution of the both explanatory variables were different among aboveground biomass production variables. That is, mass ratio mechanism by community weighted mean values with dominant traits was a main driver for initial and last aboveground biomasses and the increment of aboveground biomass by survivors and recruits, whereas aboveground biomass loss by mortality of stems was govern by species diversity. The mechanism controlling the loss of aboveground biomass associated with species diversity may relate to size-dependent demographic processes of individual woody stems, especially, the withering of canopy trees. Therefore, our results suggest that mass ratio and size-dependent mechanisms of woody plants may be important factors shaping the aboveground biomass productions in our study site. In this study, we assessed the relationships between species and functional diversity indices and aboveground biomass production variables but we didn't consider the effects of environmental (e.g., soil properties) and intrinsic (e.g., forest ages, site history) variables. Recently, leading studies have reported that biomass dynamics can be influenced by a series of environmental conditions, forest ages, stochastic events and historical factors (Wu *et al*., 2015; Poorter *et al*., 2017). Therefore, it needs to implement further studies on the importance and role of these variables for biomass dynamics to better understand ecosystem functions and processes.

Acknowledgements: We thank Dr. Joon-Hwan Shin and Dr. Hyun-Je Cho for invaluable help during fieldwork and data analysis. This study was carried out with the support of 'R&D Program for Forest Science Technology (Project No. 2019150C10-1923-0301)' provided by Korea Forest Service (Korea Forestry Promotion Institute).

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Appendix 1. Functional trait data and abundance of woody plant species recorded between the first (1997) and last (2017) censuses at the long-term ecological research site in Mt. Gyebang, South Korea.

Family name	Scientific name[1]	Functional trait data[2]				Source for functional trait data[3]			Census year	
		LF	MH (m)	LS (cm)	WD (g/cm^3)	LF & MH	LS	WD	1997	2017
Anacardiaceae	*Toxicodendron trichocarpum*	T	7	11	0.62	(4)	(4)	(9)	3	1
Araliaceae	*Aralia elata*	S	11.7	13	0.42	(4)	(4)	(9)	24	-
Araliaceae	*Kalopanax septemlobus*	T	25	40	0.57	(4)	(4)	(6)	96	71
Betulaceae	*Alnus maximowiczii*	T	10	14	0.54	(4)	(4)	(6)	3	-
Betulaceae	*Betula costata*	T	30	8.9	0.63	(4)	(4)	(6)	2	-
Betulaceae	*Betula schmidtii*	T	30	9.75	0.87	(4)	(4)	(6)	138	110
Betulaceae	*Carpinus laxiflora*	T	24.3	8.75	0.68	(4)	(4)	(6)	2	2
Betulaceae	*Corylus heterophylla*	S	5.7	17	0.49	(4)	(4)	(9)	18	1
Celastraceae	*Euonymus macropterus*	S	10	13.5	0.61	(4)	(4)	(9)	-	3
Celastraceae	*Euonymus oxyphyllus*	S	18.1	11	0.61	(4)	(4)	(9)	15	15
Celastraceae	*Euonymus verrucosus*	S	6.5	10	0.61	(5)	(5)	(9)	10	8
Cornaceae	*Cornus controversa*	T	20	14	0.56	(4)	(4)	(6)	17	12
Ericaceae	*Rhododendron schlippenbachii*	S	6.9	12	0.50	(4)	(4)	(9)	-	19
Fagaceae	*Quercus mongolica*	T	30	17.5	0.78	(4)	(4)	(6)	527	304
Juglandaceae	*Juglans mandshurica*	T	20	27.5	0.5	(4)	(4)	(6)	3	2
Lauraceae	*Lindera obtusiloba*	S	6	18.5	0.52	(4)	(4)	(6)	-	17
Leguminosae	*Maackia amurensis*	T	20	8.75	0.55	(4)	(5)	(6)	59	17
Magnoliaceae	*Magnolia sieboldii*	T	10	18	0.50	(4)	(4)	(9)	277	191
Malvaceae	*Tilia amurensis*	T	20	11	0.35	(4)	(4)	(6)	459	303
Malvaceae	*Tilia mandshurica*	T	18.4	22.5	0.35	(4)	(4)	(7)	10	3
Moraceae	*Morus australis*	T	11.5	19.75	0.62	(4)	(4)	(9)	6	6
Oleaceae	*Fraxinus chinensis* subsp. *rhynchophylla*	T	20.9	15.5	0.69	(4)	(4)	(6)	97	38
Pinaceae	*Abies holophylla*	T	40	4.2	0.38	(4)	(4)	(6)	95	89
Pinaceae	*Pinus densiflora*	T	35	11.15	0.44	(4)	(4)	(6)	122	75
Pinaceae	*Pinus koraiensis*	T	30	9.65	0.43	(4)	(4)	(6)	99	103
Rosaceae	*Prunus sargentii*	T	20	15.5	0.59	(4)	(4)	(6)	3	2
Rutaceae	*Phellodendron amurense*	T	10	11.5	0.39	(4)	(4)	(7)	1	-
Salicaceae	*Populu stremula* var. *davidiana*	T	14.5	7.5	0.40	(4)	(4)	(7)	19	5
Sapindaceae	*Acer mandshuricum*	T	10	9.5	0.72	(4)	(4)	(6)	1	-
Sapindaceae	*Acer pictum*	T	30	14.5	0.66	(4)	(4)	(6)	86	57
Sapindaceae	*Acer pseudosieboldianum*	T	20	17	0.54	(4)	(4)	(9)	735	861
Staphyleaceae	*Staphylea bumalda*	S	5	9	0.56	(4)	(4)	(6)	-	1
Styracaceae	*Styrax obassis*	T	14	18.5	0.44	(4)	(4)	(9)	15	16
Ulmaceae	*Ulmus davidiana* var. *japonica*	T	30	10.5	0.64	(4)	(5)	(6)	16	8
Ulmaceae	*Ulmus laciniate*	T	20	27.5	0.46	(4)	(4)	(7)	45	23

Note: [1]Scientific names follow the National Plant Species Database System (http://www.nature.go.kr).[2]Abbreviations: LF, life form; MH, maximum height; LS, leaf size as the sum of leaf length and width; WD, Wood density; T, tree; S, shrub.[3]Sources for functional traits came from several literatures and open access online databases as follows: 1) Kim, D.H., J.H. Song, K.W. Chang and J.C. Lee (2010). Seeds of woody plant in Korea. National Institute of Forest Science, Seoul (Republic of Korea); 2) Royal Botanic Gardens Kew. (2016). Seed Information Database (SID). Version 7.1. (http://data.kew.org/sid/); 3) Mean value in same genus from SID of Royal Botanical Gardens Kew; 4) Korea National Arboretum. (2014). Korea Biodiversity Information System (http://www.nature.go.kr); 5) National Institute of Biological Resources. (2011). Korea Species Database (http://species.nibr.go.kr); 6) Jung, S.H. and B.S. Park (2008). Wood characteristics of Korean useful tree species. National Institute of Forest Science, Seoul (Republic of Korea); 7) World Agroforestry Centre (2007). ICRAF Wood Density Database (http://db.worldagroforestry.org); 8) Zanne, A.E., G. Lopez-Gonzalez, D.A. Coomes, J. Ilic, S. Jansen, S.L. Lewsi, R.B. Miller, N.G. Swenson, M.C. Wiemann and J. Chave (2009). Global Wood Density Database (http://hdl.handle.net/10255/dryad.235); 9) Mean value in same genus from ICRAF Wood Density Database.