

Youngil Kim · Sinkyu Kang · Jong-Hwan Lim
Dowon Lee · Joon Kim

Inter-annual and inter-plot variations of wood biomass production as related to biotic and abiotic characteristics at a deciduous forest in complex terrain, Korea

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Abstract This study aims to evaluate inter-annual and inter-plot variation of wood biomass production (WBP) and to investigate the relationships of the WBP variations with several biotic and abiotic characteristics at a deciduous forest in complex terrain, the Gwangneung Experimental Forest, Korea. Based on field survey in the plot-scale study area, WBP during 1991–2004 was estimated by a dendrochronological method. Our field data indicated that the inter-annual variation of WBP was closely related to the seasonal climate of both winter air temperature and spring precipitation. The inter-plot variation of WBP was highly associated with basal area, biomass, and frequency of *Quercus* spp. in the plots, and correlations of the inter-plot variation with the stand characteristics of the specific species were stronger than those with slope and soil water content. Our results suggest that the annual fluctuation of forest productivity is primarily governed by severe climate in a season of the year, and the spatial distribution of a dominant species largely represent plot variation in the productivity.

Our findings contribute to an enhanced understanding of climatic effects on the annual variability of forest productivity and the spatial heterogeneity of the productivity, which are extensively concerned with forested ecosystems of Korea.

Keywords Wood biomass production · Inter-annual and inter-plot variation · Complex terrain · Forest stand characteristics · Meteorology · Topography

Introduction

Global forested areas are regarded as important land covers in global carbon cycling due to their roles as CO₂ sinks (Goodale et al. 2002; Cook et al. 2004; McCaughey et al. 2006). In East Asia, forested areas are mainly located within the complex terrain of mountainous regions because of high socio-economic pressure on land use (Skeldon 1985). Complex terrain represents ca. 20% of the earth's terrestrial surface, and these regions are critical for providing timber, aesthetic appreciation, and fresh water for at least half of humankind (Becker and Bugmann 1997; Mountain Agenda 1998). Carbon cycles or specific components of carbon cycles on forest ecosystems have been monitored in many studies using field inventory surveys (e.g., Jenkins et al. 2001; Zhao and Zhou 2005), eddy-covariance systems (e.g., Massman and Lee 2002; Schmid et al. 2003), ecosystem models (e.g., Kimball et al. 1997; Sitch et al. 2003), and satellite remote sensing (e.g., Field et al. 1995; Turner et al. 2003). They have provided reliable predictions for carbon cycles on forest ecosystems in recent times. Among components in the carbon cycle, net primary production (NPP, g C m⁻² year⁻¹) have been well evaluated by applying field inventory surveys (Jenkins et al. 2001), and gross primary production (GPP, g C m⁻² year⁻¹) and net ecosystem production (NEP, g C m⁻² year⁻¹) were reasonably evaluated using eddy-covariance systems

Y. Kim · D. Lee
Graduate School of Environmental Studies,
Seoul National University, Seoul 151-742, Republic of Korea

S. Kang (✉)
Department of Environmental Science,
Kangwon National University, Chuchon,
Kangwon-do 200-701, Republic of Korea
E-mail: kangsk@kangwon.ac.kr
Tel.: +82-33-2508578

J.-H. Lim
Department of Forest Environment,
Korea Forest Research Institute (KFRI), Seoul 130-712,
Republic of Korea

J. Kim
Department of Atmospheric Sciences, Yonsei University,
Seoul 120-749, Republic of Korea

Present address: Y. Kim
Department of Geography, McGill University, Montreal,
QC H3A 2K6, Canada

(Schmid et al. 2003). Ecosystem models and satellite remote sensing have been accepted as a useful tool for estimating all of the components (Kimball et al. 1997; Turner et al. 2003). Nevertheless, in the complex terrain regions, our understanding of carbon cycles is still limited due to difficulties in access and interpretation of eddy-covariance tower data, and complex interactions between water and carbon cycles for ecosystem modeling, and topographic effects on remote sensing data. In comparison to these restrictions, field inventory data from direct measurements generally support knowledge about carbon cycles in complex terrains on forest ecosystems.

In a forest region, NPP is broadly used as a main indicator of the sequestration of atmospheric CO₂ by the ecosystem (Cao and Woodward 1998; Gower et al. 1999). In addition to the direct field measurement method, modeling approaches (ecosystem model and remote sensing) have widely predicted NPP at various spatial scales, from plot to regional scale (Ito and Oikawa 2000; Turner et al. 2002; Ahl et al. 2004; Kang et al. 2006a). The reliability of the predicted NPP can be validated with field measurements. However, because NPP measurements are expensive, laborious, time-consuming, as well as destructive, the limited measured data sometimes provide poor validations (Okubo 1980; Liu et al. 2002). Especially, the model validation for a complex terrain watershed is more problematic due to the considerable spatial variation found in such a watershed. Hence, a better interpretation about spatial variation of NPP within the watershed is necessary in order to properly use field NPP data for the model validations.

A number of studies have examined the dominant biotic and abiotic environmental variables affecting spatial and temporal variation of forest NPP. The temporal NPP variations were well correlated with fluctuations in air temperature, precipitation, and solar radiation (Ogaya et al. 2003; Kang et al. 2006b; Tardif and Conciatori 2006). In contrast, the spatial NPP variations were more explained by biotic characteristics, including leaf area index (LAI, m² m⁻²), stand ages, and species compositions (Jenkins et al. 2001; Burrows et al. 2003; Van Tuyl et al. 2005). Some studies have shown that gradients of meteorological variables played an important role in determining the spatial patterns of NPP in a regional-scale area (Villalba et al. 1994; Andreassen et al. 2006) and a topographically complex watershed (Eum et al. 2005; Chen et al. 2007). Soil water content (SWC, %) was also suggested as one of the primary abiotic characteristics triggering spatial variation of NPP in a forested landscape (Cantón et al. 2004; Newman et al. 2006). This evidence indicates that forest NPP is highly heterogeneous, and spatial and temporal NPP variations are influenced by changes in biotic and abiotic conditions, which vary spatially in a complex terrain watershed.

Generally, NPP is divided into three components: wood biomass production (WBP) (representing net

growth of stems, branches, and coarse roots), leaf production, and fine root production (Clark et al. 2001). Because WBP comprises over a third of NPP, accurate measurements of WBP are especially important for estimating NPP (Kopp et al. 1996; Jenkins et al. 2001). Long-term retrospective WBP can be determined by applying allometric equations and dendrochronological methods (extracting tree increment cores to estimate tree growths). This technique was used to extend WBP measurements to a larger area and a longer period (Tickle et al. 2001; Ohtsuka et al. 2005), and thus it can be useful to examine spatial and temporal NPP variations in complex terrain watersheds.

In this study, we evaluated inter-annual and inter-plot variation of WBP in a well-reserved Korean deciduous hardwood forest within a complex terrain. The WBP data was determined using the dendrochronological method and utilized to identify major biotic and abiotic characteristics concerning the inter-annual and inter-plot NPP variations. Most of the Korean forests are contained in mountainous regions, which were intensively planted 30–50 years ago after massive destruction of the forests due to forest exploitation (1919–1945) and the Korean War (1950–1953) (Choi et al. 2002). In accordance with growing the young forests, these regions are expected to have biological and environmental succession. Therefore, studies in the reserved forest will reflect the future stages of the young forests in terms of forest productivity. Based on the previous literature, it was hypothesized that the inter-annual NPP variation was strongly related to the temporal variations in climate, while the inter-plot NPP variation was closely associated with forest stand attributes (e.g., species composition), as well as topography-generated variables (e.g., SWC). To test our hypotheses, we used long-term WBP data to determine magnitudes of the inter-annual and inter-plot WBP variation and to investigate the effects of the inter-annual climatic variability on WBP and the relationships of the inter-plot variation with biotic and topographic characteristics.

Materials and methods

Study area

This study was carried out in a deciduous broadleaf forest (DBF) watershed in the Gwangneung Experimental Forest (GEF), located in the west-central part of the Korean Peninsula (N 37°44', E 127°09') (Fig. 1). The DBF watershed lies in a typical cool-temperate broad-leaved forest zone. The forest, dominated by *Quercus acutissima*, *Carpinus cordata*, and *Carpinus laxiflora*, is characterized by different stand ages and disturbance history. The trees are between 80 and 200 years old with a canopy height of 18–20 m. The forest may have been exposed to fires in the past although none has been recorded. The study watershed covers 22 ha in area, and

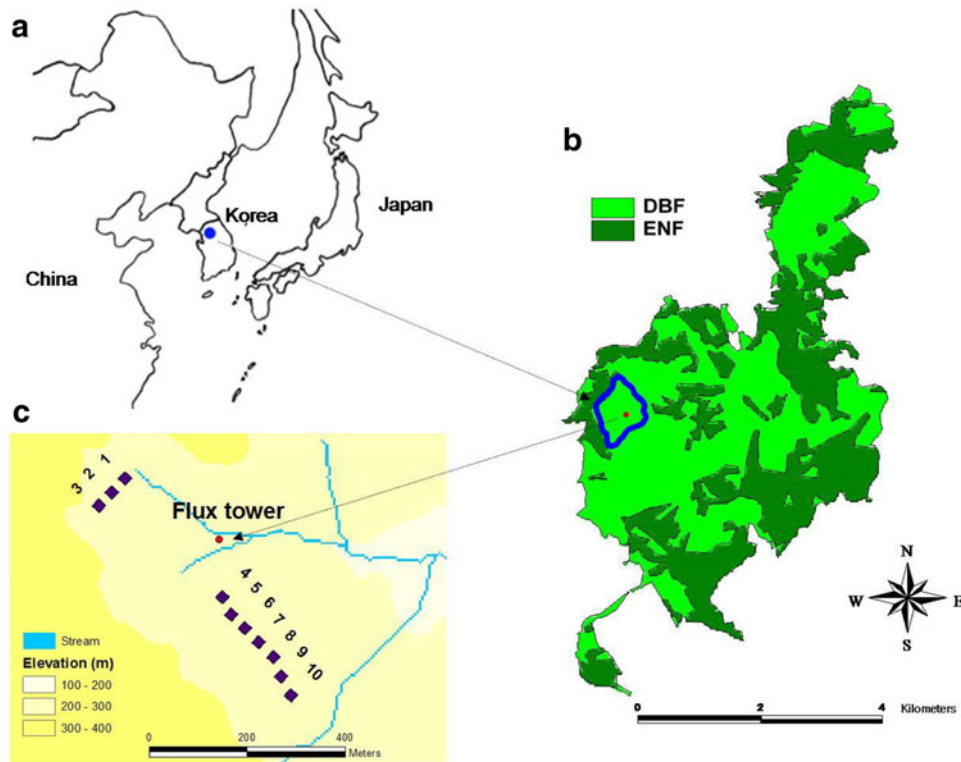


Fig. 1 Descriptions of the study area: **a** map of East Asia; **b** forest map of the Gwangneung Experimental Forest (GEF) including the study watershed (inside the thick line), classified as deciduous

broadleaf forests (DBF) and evergreen needleleaf forests (ENF); and **c** locations of the study plots (no. 1–10) and the eddy covariance flux tower on the forest stands

elevation ranges 210–530 m. Soil in this watershed is classified as brown forest soil (mostly Inceptisols) developed on granite gneiss (Lim et al. 2003). The DBF watershed was designated not only as one of the Korean long-term ecological research (KLTER) sites by the Korea Forest Research Institute (KFRI) since 1998 (Oh et al. 2000), but also as a site in the KoFlux network (<http://www.koflux.org/>) (Kim et al. 2006). The 30-year mean annual air temperature is 10.2°C, and the 30-year mean annual precipitation is 1,365 mm, of which approximately two-thirds fall during the Korean monsoon season (late June–middle July) (Kang et al. 2003). Though we do not have snowpack data from the site, this mountainous area is generally covered with snowpack during winter seasons. During the last 10 years, mean annual snowfall measured at nearby Dongduchun National Weather Station, placed 16 km away from the GEF, is 328 mm (data from Web site of the Korean Meteorological Administration, <http://www.kma.go.kr/>).

We delineated ten study plots along the two eastern-facing slopes within the watershed, based on considerations of difference in slope and dominant tree species (Fig. 1). The size of each plot is 20 × 20 m, and the distance between the plots on each slope was set as 20 m. The plots have different slopes, ranging from 10 to 35°, and species compositions but similar aspect (northeast and east) and elevation (227–287 m) (Table 1). The reason of determining the plot size was partially

involved with difficulty to carry out labor-intensive field works (tree survey and core extraction). Although the size of our total study area (0.4 ha) was smaller than that of the previous survey area (1 ha) in the GEF deciduous watershed (Lim et al. 2003), tree distribution and biomass in this study were almost the same compared to those found in Lim et al. (2003). It could indicate properness in our plot design as representing forest tree composition in the watershed. Both our study and that of Lim et al. (2003) showed that QS (*Quercus* spp.), CL (*Carpinus laxiflora*), and CC (*Carpinus cordata*) were the dominant species (higher dominant in an order), which was determined by larger values in the basal area. Total biomass in this study was 30.5 kg m⁻² (Table 1), but that in Lim et al. (2003) was 26.1 kg m⁻². The dominant species of QS (60%), CL (15%), and CC (10%) was mostly composed of total biomass in the study plots. Similarly, the three species (QS: 57%; CL: 21%; and CC: 6%) largely comprised total biomass in the former study area (Lim et al. 2003).

Meteorological and field-measured data

We prepared daily meteorological data detailing mean/maximum/minimum air temperature (°C), total precipitation (cm), mean vapor pressure deficit (VPD, Pa), daytime mean incident shortwave radiation (W m⁻²),

Table 1 Description of topography and species composition in the study area

| Plot no. | Elevation (m) | Aspect | Slope topography | Slope (°) | SWC (%) | Basal area (cm ² m ⁻²) | | | | | Biomass (kg m ⁻²) | | | | |
|----------|---------------|--------|--------------------------|-----------|---------|---|------|------|------|------|-------------------------------|------|-----|------|------|
| | | | | | | QS | CL | CC | OS | Sum | QS | CL | CC | OS | Sum |
| 1 | 279 | E | Upper-side ^a | 22.5 | 18.1 | 19.2 | 6.0 | 1.0 | 2.7 | 28.9 | 19.1 | 4.8 | 0.6 | 1.5 | 26.0 |
| 2 | 282 | E | Upper-side ^a | 32.5 | 21.8 | 9.4 | 11.0 | 2.3 | 2.4 | 25.1 | 9.2 | 8.6 | 1.3 | 1.5 | 20.6 |
| 3 | 287 | SE | Upper-side ^a | 32.5 | 19.2 | 25.1 | 14.8 | 0.7 | 0.3 | 40.9 | 23.4 | 11.7 | 0.4 | 0.1 | 35.6 |
| 4 | 227 | NE | Lower-side ^b | 17.5 | 23.6 | 15.7 | 9.1 | 3.4 | 9.4 | 37.6 | 14.8 | 7.7 | 2.3 | 7.3 | 32.1 |
| 5 | 240 | NE | Lower-side ^b | 12.5 | 23.7 | 28.6 | 0.0 | 1.0 | 1.5 | 31.1 | 34.6 | 0.0 | 0.6 | 0.7 | 36.0 |
| 6 | 242 | E | Crest ^c | 17.5 | 21.2 | 0.0 | 8.6 | 5.1 | 6.7 | 20.4 | 0.0 | 8.6 | 4.0 | 6.0 | 18.6 |
| 7 | 244 | NE | Middle-side ^c | 17.5 | 22.1 | 28.6 | 0.0 | 5.8 | 3.4 | 37.8 | 30.9 | 0.0 | 4.1 | 1.7 | 36.6 |
| 8 | 245 | E | Crest ^b | 22.5 | 17.5 | 8.8 | 0.0 | 4.7 | 4.3 | 17.8 | 9.8 | 0.0 | 3.4 | 1.9 | 15.1 |
| 9 | 250 | E | Middle-side ^b | 12.5 | 20.2 | 16.6 | 0.1 | 11.6 | 10.9 | 39.2 | 18.6 | 0.0 | 8.6 | 9.2 | 36.5 |
| 10 | 253 | NE | Middle-side ^c | 22.5 | 19.5 | 20.1 | 4.2 | 9.8 | 14.3 | 48.3 | 22.9 | 4.0 | 6.9 | 14.4 | 48.3 |
| Mean | 255 | – | – | 21.0 | 20.7 | 17.2 | 5.4 | 4.6 | 5.6 | 32.7 | 18.3 | 4.5 | 3.2 | 4.4 | 30.5 |

SWC indicates soil water content, abbreviations in species groups are QS, *Quercus* spp.; CL, *Carpinus laxiflora*; CC, *Carpinus cordata*; and OS, 12 species except for QS, CL, and CC

^a Ridge position

^b Slope position

^c Valley position

rainfall frequency, and aridity index from 1990 to 2004. In the GEF, precipitation has been measured since 1982, but air temperature has only been recorded since 1999. Hence, we estimated air temperatures during 1990–1998 using a linear regression model between the GEF's temperature data and the measurements at the Dongdunchun National Weather Station. Coefficients of determination (r^2) of the regression models were 0.99 for both daily maximum and minimum air temperature.

Daily mean air temperature, shortwave radiation, and VPD were estimated using a synoptic micrometeorological model, MTCLIM v.4.3 (Running et al. 1987) with inputting the prepared maximum/minimum air temperature and precipitation. MTCLIM was developed to predict micrometeorological variables in mountainous areas, and the model's outputs were well validated in various regions (e.g., Running et al. 1987; Thornton et al. 2000). Two additional meteorological variables used in this study were rainfall frequency and aridity index. Here, rainfall frequency and aridity index indicate a number of rainy days and sum of precipitation (cm) divided by mean air temperature (°C) + 10 (de Martonne 1926) in a specific period (month, season, or year), respectively.

All of the meteorological data were temporally classified as three categories: yearly, seasonal, and monthly periods. Seasonal periods were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). For the specific period, air temperatures, shortwave radiation, and VPD were averaged, while precipitation and rainfall frequency were summed. Lastly, the aridity index was determined using the averaged mean temperature and the summed precipitation.

In the study plots, survey of tree composition and tree core extractions were conducted in October, 2005. All of the trees over 2 cm in diameter at breast height (DBH) (259 individuals) were investigated as recording their

species names and DBH, and the cored individuals were randomly selected among the trees over 5 cm in DBH (122 individuals), which was approximately half of the recorded individuals (Table 2 in Appendix). Increment boring was performed on the selected cored individuals using an increment borer at the southern direction. A length of 7 cm of tree core was taken per individual. We assumed that collection of one core at the same direction could represent variability of the core-derived data within the study region.

The measurement of SWC was conducted in April, 2006, which was a warm and dry season of Korea. CD620 HydroSense (Campbell Scientific Inc., Logan, UT, USA) with a 12-cm probe was used for our measurement. Nine measurement points were randomly selected in each plot with considering distance between trees, and then five repeated measurements were carried out at each point. The representative SWC of each plot was finally derived from averaging the repeated point SWC data. We collected the data one time because our previous SWC measurements in spring covering topographic gradients from the DBF watershed showed consistent spatial patterns with different ranges (unpublished data).

Dendrochronological analyses and WBP estimates

The collected core samples were air-dried for 2 days and then mounted on wooden trays attached with transparent epoxy adhesive in the laboratory. Annual growth of radial widths was measured to a unit of 0.01 mm using the LINTAB (Frank Rinn Inc., Heidelberg, Germany). The cross-dating method was used to ensure the temporal consistency of patterns in the measured annual growth. Since 12 cores containing vague tree rings were discarded in the measurements, 110 core samples among 122 cores were finally utilized to determine the annual diameter growths of trees. These dendrochronological

analyses were technically supported by the Bank of Dendrochronological Database in Chungbuk National University, Korea.

WBP in each plot was estimated by summing annual wood biomass growth (kg year^{-1}) (subtracting previous-year biomass from current-year biomass) of all individuals in the plots. Allometric equations and regression methods were adopted to estimate individual biomass of trees in each year from 1990 to 2004. We used the allometric equations for high and low wood density species, developed from field surveys in the GEF by Lim (1998). The equations can calculate wood biomass (kg) of both above and below ground from DBH inputs (cm). For the high-wood-density species of deciduous species in the GEF (e.g., *Acer* spp., *Carpinus* spp., *Fraxinus* spp., and *Quercus* spp.), the allometric equation of $\text{biomass} = 0.1673 \times \text{DBH}^{2.393}$ is applied, while another allometric equation, $\text{biomass} = 0.086 \times \text{DBH}^{2.393}$, is utilized for the low-wood-density species, such as *Cornus* spp. and *Pinus* spp. (Lim 1998; Lim et al. 2003).

For the cored trees, DBH during 1990–2004 was retrospectively identified based on the annual radial growths from the tree cores. These DBH values were directly applied in the allometric equations to estimate annual wood biomass. However, for the uncored trees, annual wood biomass growth was indirectly estimated from empirical regression methods between measured DBH in 2005 and the estimated biomass growth for each year of 1991–2004 in the cored trees. Since the number of core samples ($n = 110$) was insufficient for applying the methods to all 17 species found in the study area, we categorized four species groups considering the dominant species and numbers of the core samples: QS ($n = 23$), CL ($n = 25$), CC ($n = 31$), and OS (12 species of other than QS, CL, and CC, $n = 31$). For each tree category and year, we developed an empirical model using DBH of year 2005 and the wood growth of the cored trees (Table 3 in Appendix). These models and DBH of uncored trees were then used to estimate the amounts of the biomass growth for the uncored trees. Finally, the annual biomass growth for cored and uncored individuals was integrated as plot-scale WBP. In this study, we presumed 50% of the vegetation biomasses consisted of carbon contents, and WBP was expressed as a unit of $\text{g C m}^{-2} \text{ year}^{-1}$.

Statistical analyses

We performed one-way analysis of variance (ANOVA) tests to examine significance of the inter-annual WBP variation about the study years and the inter-plot WBP variation about the plots. For the test of the inter-plot variation, 14-year mean WBP of each plot ($n = 14$) (Plot-WBP, the last column of Table 4 in Appendix) was prepared, whereas 10-plot mean WBP of each year ($n = 10$) (Year-WBP, the last row of Table 4 in Appendix) was prepared for the inter-

annual variation test. Coefficient of variation (CV, %) was used to determine the magnitudes of the inter-annual and inter-plot WBP variation and relative importance between the two variations. We calculated 14-year mean CV of each plot ($n = 14$) (Year-CV) and 10-plot mean CV of each year ($n = 10$) (Plot-CV) to represent the inter-annual and inter-plot variations, respectively.

The biotic and abiotic characteristics affecting the WBP variations were identified based on correlation analyses using the forest stand attributes and the environmental variables of meteorology and topography. The stand attributes include basal area, biomass, and number and frequency of trees in each of the species groups, and the environmental variables detail yearly, seasonal, and daily meteorological data, and slope and SWC. SPSS for Windows, Release 15.0 (SPSS Inc., Chicago, IL, USA) was used in the statistical analyses.

Results

Inter-annual and inter-plot WBP variation and relationships with stand characteristics

From 1991 to 2004, WBP was averaged as $271.4 \text{ g C m}^{-2} \text{ year}^{-1}$. Year-WBP was minimum ($188.7 \text{ g C m}^{-2} \text{ year}^{-1}$) in 2001 and maximum ($304.7 \text{ g C m}^{-2} \text{ year}^{-1}$) in 1999 (Fig. 2a). Except for the year 2001, Year-WBP was fluctuated within a range of $50 \text{ g C m}^{-2} \text{ year}^{-1}$. Plot-WBP ranged from $125.3 \text{ g C m}^{-2} \text{ year}^{-1}$ (plot 6) to $349.2 \text{ g C m}^{-2} \text{ year}^{-1}$ (plot 4) (Fig. 2b). All of the values of plot-level WBP during the study period were present in Table 4 in Appendix.

The ANOVA tests showed that there was significant inter-plot WBP variation ($p < 0.001$) but insignificant inter-annual WBP variation ($p = 0.56$) in the study region. Similarly, the CV values presented importance of the inter-plot variation. Plot-CV showed a mean of 33%, and ranged from 29% (2001) to 36% (1998), while averaged Year-CV was 10%. The minimum value of Year-CV was 7% (plot 1), and the maximum value resulted in 20% (plot 9). In the ANOVA and CV analyses, the inter-plot variation was greater than the inter-annual variation.

Among forest-stand characteristics in the species groups, the characteristics in the QS group were only significantly associated with the inter-plot WBP variation. Our regression tests appeared that each of the basal area ($r = 0.75$), biomass ($r = 0.71$), and frequency of trees ($r = 0.64$) in the QS group were positively correlated with Plot-WBP with the significant level ($p < 0.05$) (Fig. 3). Linear functions indicated the best-fitted regressions between Plot-WBP and the QS characteristics of basal area ($\text{WBP} = 7.18 \times \text{basal area} + 147.74$, $r^2 = 0.56$), biomass ($\text{WBP} = 6.06 \times \text{biomass} + 160.36$, $r^2 = 0.51$), and frequency of trees ($\text{WBP} = 6.33 \times \text{frequency} + 189.65$, $r^2 = 0.41$).

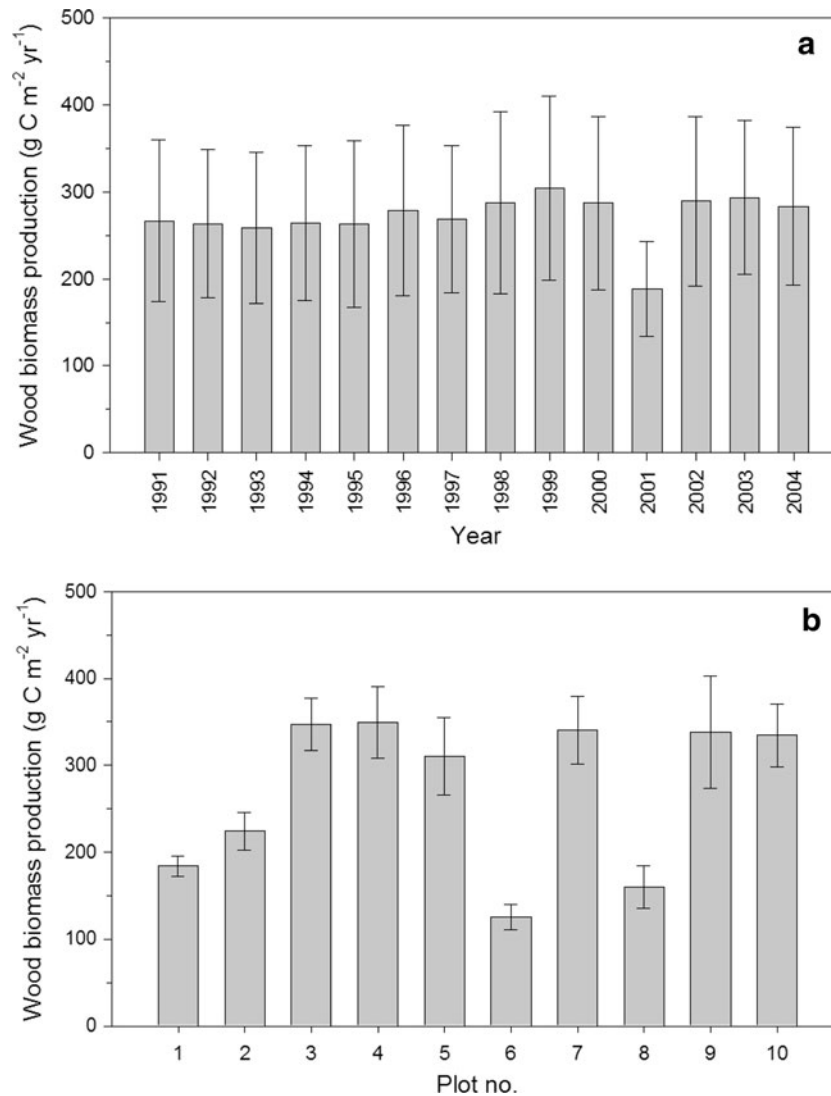


Fig. 2 Means and standard deviations (*upper and lower bars*) of **a** 10-plot mean wood biomass production of each year (Year-WBP, g C m⁻² year⁻¹) during 1991–2004 and **b** 14-year mean wood

biomass production of each plot (Plot-WBP, g C m⁻² year⁻¹) from plot 1 to plot 10

Relations of WBP variations with environmental variables

Our analyses showed that the inter-annual WBP variation was primarily associated with temperature-related variables in current-year winter and water-related variables in current-year spring. Among the seasonal meteorological variables, each of mean air temperature ($r = 0.66$, $p < 0.05$) and maximum air temperature ($r = 0.60$, $p < 0.05$) in current-year winter had significant positive correlation with Year-WBP (Fig. 4a), and aridity index ($r = -0.61$, $p < 0.05$) in current-year winter presented considerable negative correlation with Year-WBP. Similarly, in current-year spring, aridity index ($r = 0.57$, $p < 0.05$), precipitation ($r = 0.60$, $p < 0.05$), and rainfall frequency ($r = 0.57$, $p < 0.05$) showed positive correlations with Year-WBP (Fig. 4b), but shortwave radiation ($r = -0.75$, $p < 0.01$) showed

negative correlations. Furthermore, according to the correlation tests using the monthly variables, air temperatures in current-year January were closely relevant with Year-WBP (mean temperature: $r = 0.70$, $p < 0.05$; maximum temperature: $r = 0.70$, $p < 0.05$; minimum temperature: $r = 0.58$, $p < 0.05$). In the spring season, strong positive relationships were found between Year-WBP and the aridity index ($r = 0.61$, $p < 0.05$), and precipitation ($r = 0.62$, $p < 0.05$) in current-year April. Also, shortwave radiation in current-year April ($r = -0.78$, $p < 0.01$) and VPD in current May ($r = -0.59$, $p < 0.05$) were significantly negatively related to the WBP. However, in the yearly correlation analyses, none of the meteorological variables was strongly correlated with Year-WBP (Fig. 4c, d).

Using the plot slope and SWC data, correlations with Plot-WBP were analyzed to investigate the inter-plot WBP variation related to the topographic characteristics.

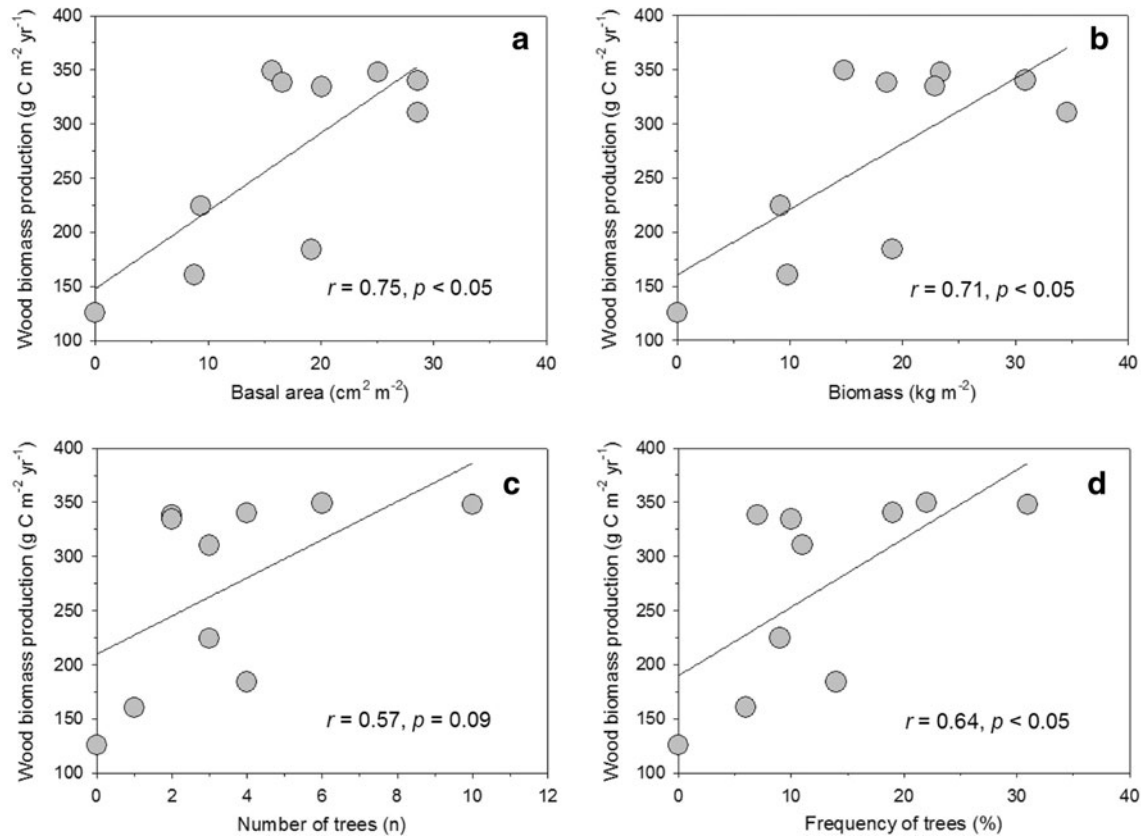


Fig. 3 Relationships between 14-year mean wood biomass production of each plot (Plot-WBP, $\text{g C m}^{-2} \text{ year}^{-1}$) and **a** basal area ($\text{cm}^2 \text{ m}^{-2}$), **b** biomass (kg m^{-2}), **c** number of investigated trees (n)

in each 0.04 ha plot, and **d** frequency of investigated trees (%) of the QS group (*Quercus* spp.) in each plot from plot 1 to plot 10

Here, only the SWC data showed significant spatial heterogeneity (one-way ANOVA, $p < 0.001$). From the correlation tests, slope was poorly associated with Plot-WBP ($r = -0.14$, $p = 0.71$). SWC was also insignificantly concerned with the inter-plot WBP variation ($r = 0.39$, $p = 0.26$). We analyzed again with SWC dataset without plot 6 because plot 6 contained a small gully inside, which assumed to provide the poorly representative observation of SWC. This attempt exhibited a higher relationship ($r = 0.55$, $p = 0.13$) between the two variables but still showed the statistically insignificant level.

Discussion

In Korea, most of the forests are 30 to 50-year-old secondary forests resulting from successful government-driven plantation activity since the early 1960s, and these young forests are characterized by high wood productivity with low biomass (Choi et al. 2002). In contrast, our study area of the GEF watershed is a well-reserved forest, containing lower wood productivity ($271.4 \text{ g C m}^{-2} \text{ year}^{-1}$) with higher biomass (30.5 kg m^{-2}) when compared to the values of 26 to 50-year-old planted *Quercus* forests in central Korea (481.3 g C

$\text{m}^{-2} \text{ year}^{-1}$ with 19.0 kg m^{-2}) (Kwak and Kim 1992; Park et al. 2003). This indicates much less wood productivity per unit biomass (8.9 g C kg^{-1}) in our study region than that (25.3 g C kg^{-1}) in the young *Quercus* stands.

The WBP estimates based on our dendrochronological analyses agreed well with those determined by DBH increment measurements for 20 trees located in the study forest (*Quercus acutissima*: $n = 7$; *Carpinus laxiflora*: $n = 8$; and *Carpinus cordata*: $n = 5$) of which DBH of the year 2005 is 15.4–67.1 cm (unpublished data). To compare between the two methods, we selected 51 trees of similar DBH of the year 2005 (16.5–67.0 cm) (*Quercus acutissima*: $n = 19$; *Carpinus laxiflora*: $n = 14$; and *Carpinus cordata*: $n = 18$) among our investigated trees. During 2000–2004, mean DBH growth for the trees exhibited no significant difference (t test, $p = 0.82$), and inter-annual variation of WBP during 2000–2004 was well coincident between the two methods. They support appropriateness of our tree-core sampling and dendrochronological analyses conducted in this study and reinforce again usefulness of dendrochronology in the researches for forest growth and production in complex terrains (e.g., Seo et al. 2000; Lafon 2004).

Previous studies in the Korean deciduous forests, based on the ecosystem modeling and field observations

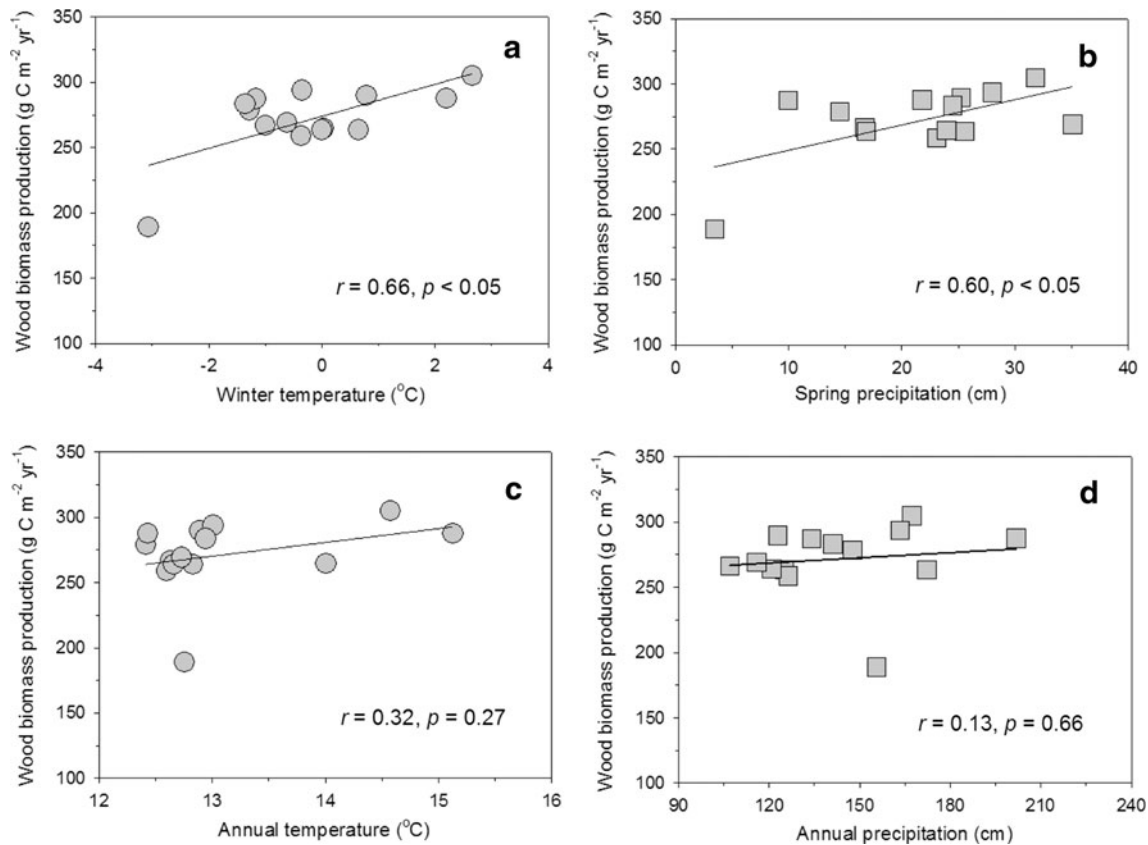


Fig. 4 Relationships between seasonal and annual temperature (round dots) and precipitation (square dots), and 10-plot mean wood biomass production of each year (Year-WBP, $\text{g C m}^{-2} \text{ year}^{-1}$) from 1991 to 2004. Seasonal variables includes **a** current-year winter mean temperature (winter temperature, $^{\circ}\text{C}$) and **b** current-

year spring summed precipitation (spring precipitation, cm), and annual variables are **c** current-year annual mean temperature (annual temperature, $^{\circ}\text{C}$) and **d** current-year summed precipitation (annual precipitation, cm)

for a maximum of 8 years, presented that NPP was primarily controlled by amount and frequency of annual precipitation (Eum et al. 2005; Kang et al. 2006b). However, our study found that the inter-annual WBP variation was much associated with seasonal meteorology of spring precipitation and winter temperature instead of the annual variables (Fig. 4). Particularly, it seems that spring-time water supply well accounts for dramatic reduction of WBP in 2001 which found in our dendrochronological analyses (Fig. 2a). Even though annual precipitation in 2001 (156 cm) was higher than the averaged annual precipitation from 1991 to 2004 (143 cm), a severe drought occurred in the spring of 2001 compared to averaged spring precipitation for the other study years (3 vs. 23 cm) (Fig. 5a). In a watershed of the GEF including our study area, Lee et al. (2007) and Hwang et al. (2008) also reported a dramatic drop of forest productivity in 2001 from the model predictions using a well-organized eco-hydrological model, RHES-Sys (Regional Hydro-Ecologic Simulation System) (Tague and Band 2004). They provide the confidence of our WBP measurements and implicate the effects of spring drought on inter-annual variation of NPP in the GEF region.

Interestingly, current-year winter air temperature (mean and maximum temperature) was significantly positively correlated with WBP (Fig. 4a). The effect of winter temperature is identified by comparing between the inter-annual pattern of WBP and winter mean temperature (Fig. 5b): the highest WBP (1999) and the lowest WBP (2001) correspond with the year of highest and lowest winter mean temperature, respectively. Especially, mean winter temperature of 2001 (-3.1°C) is a much lower value than that of the other study years (-0.2°C). Several studies concluded that a severe winter with low temperatures increased the physiological damage of the trees, so winter temperature could be an important meteorological variable affecting forest productivity (Oleksyn et al. 1998; Elfving et al. 2001). The major harmful effect from cold winter originated from increasing pruned trees, which led to a higher rate of the pathogen infections in trees (Elfving et al. 2001).

The extremely low WBP of 2001 might have been caused by both spring drought and cold winter. The multiple linear regression using both spring precipitation and winter temperature ($WBP = 0.10 \times a + 8.64 \times b + 251.43$; a : spring precipitation (cm) and b : winter mean temperature ($^{\circ}\text{C}$)) explains the inter-annual WBP

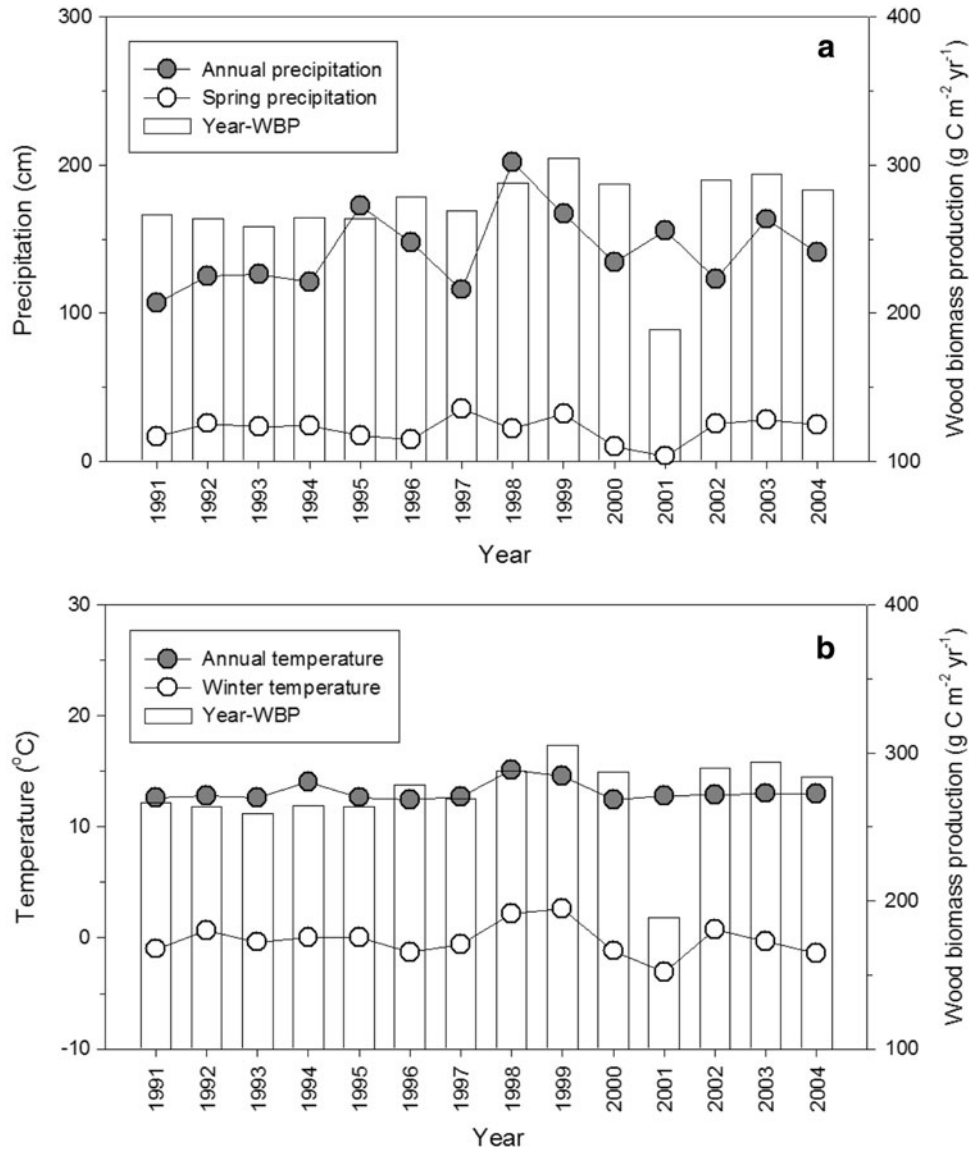


Fig. 5 a Changing patterns of annual summed precipitation (annual precipitation, cm) and spring-time summed precipitation (spring precipitation, cm), and 10-plot mean wood biomass production of each year (Year-WBP, g C m⁻² year⁻¹) and **b** the

patterns of annual averaged air temperature (annual temperature, °C) and winter-time averaged air temperature (winter temperature, °C), and Year-WBP

variation ($r^2 = 0.49$, $p < 0.05$) better than the simple regression by each variable (spring precipitation: $r^2 = 0.35$, $p < 0.05$; winter temperature: $r^2 = 0.43$, $p < 0.05$). Although further studies concerning the effects of cold winter are needed, we possibly suggest that fluctuation of NPP in the study area is interacted with spring drought and cold winter together. Therefore, this study reveals that particular meteorological variables largely affect amounts of productivity in forest ecosystems, which are able to enhance our understanding of meteorological controls on primary productivity.

Moreover, the annual variability of WBP is also potentially influenced by current-year spring air temperature. WBP was positively related to spring temperature in spite of there being no clear relationship between each of the temperature variables ($p > 0.05$). It

might be interpreted as spring chillness that accounts for a negative impact on forest productivity, which is supported by a finding that occurrence of frost damage in late spring (middle April–May) decreased NPP in temperate forest stands (Awaya et al. 2009). However, this study area hardly provides evidence of this frost damage because during the study period, the correlation between number of frost days (minimum air temperature $\leq 0^\circ\text{C}$) in late spring and Year-WBP is negative but at an insignificant level ($r = -0.35$, $p = 0.12$). Frost damage was reported to be more severe in trees with more leaf expansion (Awaya et al. 2009). Accordingly, to better understand frost damage on this forest ecosystem, the date of the frost event and the beginning of leaf expansion (canopy onset) need to be considered simultaneously.

Our results indicate that forest-stand attributes such as basal area, biomass, and frequency of trees in a specific species group, accounted for the inter-plot WBP variation in the study area (Fig. 3). However, slope and SWC (topography-generated variable) were weakly related to the inter-plot WBP variation, although many studies in complex mountainous areas (e.g., Anthoni et al. 1999; Kang et al. 2004; Chen et al. 2007) demonstrated strong effects of local topography on spatial distribution of NPP. This weak relation potentially originates from our small-size plot sampling. A small-size plot that contains large-size trees by chance has of course large WBP, which could blur significant effects of local topography (e.g., SWC). In addition, the local soil characteristics of texture and/or nutrient contents may be responsible for the poor relationships between our selected topographic data and WBP. Stone or boulder distribution in soil layers were coupled with soil water amounts due to occurring easier drainage under coarse soil surfaces (Eriksson and Holmgren 1996). Some parts of the study stands contain many stones, and moreover, a small gully is included in plot 6. As a result, our observation at 12 cm of soil depth might hardly represent the soil moisture conditions. It was reported that the effects of topography on forest biomass and primary productivity acted differently along a gradient of soil nutrients (Takyu et al. 2003). For a better understanding of the inter-plot variation of the productivity, investigations of the soil nutrient conditions are highly recommended.

Conclusions

This study exhibited that each of the inter-annual and inter-plot WBP variations was related to different characteristics: the inter-annual variation was signifi-

cantly concerned with the seasonality of meteorological variables (spring-time precipitation and winter-time air temperature), while the inter-plot variation was associated with biotic characteristics, including basal area, biomass, and frequency of a dominant species (*Quercus* spp.). The major implications of our results are as follows: (1) a change of climate seasonality is one of the primary concerns for understanding the response of forest productivity to the changing environment; (2) considerable spatial variation in WBP needs to be incorporated explicitly in designing field sampling for producing representative forest productivity in the complex terrains; and (3) mapping species distributions in the forested area is instrumental in spatial modeling of forest productivity based on either ecosystem models or remote sensed data. With rapid developments of ecosystem modeling and satellite remote sensing techniques for the primary productivity monitoring, our method of scaling tree-level up to plot-level WBP will provide useful information for evaluating these techniques.

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Appendix

Table 2 Summary of number and frequency of investigated trees and number of cored trees according to the species groups in the study plots

| Plot no. | Number of investigated trees (<i>n</i>) | | | | | Frequency of investigated trees (%) | | | | | Number of cored trees (<i>n</i>) | | | | |
|--------------------|---|----|----|----|-----|-------------------------------------|----|----|----|-----|------------------------------------|----|----|----|-----|
| | QS | CL | CC | OS | Sum | QS | CL | CC | OS | Sum | QS | CL | CC | OS | Sum |
| 1 | 4 | 12 | 5 | 8 | 29 | 14 | 41 | 17 | 28 | 100 | 4 | 5 | 2 | 4 | 15 |
| 2 | 3 | 16 | 11 | 5 | 35 | 9 | 46 | 31 | 14 | 100 | 2 | 8 | 6 | 3 | 19 |
| 3 | 10 | 17 | 2 | 3 | 32 | 31 | 53 | 6 | 9 | 100 | 5 | 11 | 1 | 1 | 18 |
| 4 | 6 | 5 | 5 | 11 | 27 | 22 | 19 | 19 | 41 | 100 | 4 | 2 | 2 | 5 | 13 |
| 5 | 3 | 0 | 6 | 18 | 27 | 11 | 0 | 22 | 67 | 100 | 3 | 0 | 2 | 4 | 9 |
| 6 | 0 | 2 | 6 | 13 | 21 | 0 | 10 | 29 | 62 | 100 | 0 | 1 | 1 | 4 | 6 |
| 7 | 4 | 0 | 9 | 8 | 21 | 19 | 0 | 43 | 38 | 100 | 4 | 0 | 6 | 3 | 13 |
| 8 | 1 | 0 | 7 | 10 | 18 | 6 | 0 | 39 | 56 | 100 | 1 | 0 | 3 | 5 | 9 |
| 9 | 2 | 1 | 12 | 13 | 28 | 7 | 4 | 43 | 46 | 100 | 2 | 0 | 7 | 2 | 11 |
| 10 | 2 | 1 | 13 | 5 | 21 | 10 | 5 | 62 | 24 | 100 | 0 | 0 | 5 | 4 | 9 |
| Total ^a | 35 | 54 | 76 | 94 | 259 | 13 | 18 | 31 | 39 | 100 | 25 | 27 | 35 | 35 | 122 |

The abbreviations of species groups indicate QS, *Quercus* spp.; CL, *Carpinus laxiflora*; CC, *Carpinus cordata*; and OS, 12 species except for QS, CL, and CC

^a Number of investigated trees and cored trees indicate summed values, whereas frequency of investigated trees includes averaged values

Table 3 Empirical models about the species groups (QS, *Quercus* spp.; CL, *Carpinus laxiflora*; CC, *Carpinus cordata*; and OS, 12 species expect for QS, CL, and CC) to estimate annual wood biomass growth (BG , kg year^{-1}) using a parameter (a) of diameter at breast height (DBH , cm) in the uncored individuals

| Estimate | Parameter (a) | Year | QS ($n = 23$) | | CL ($n = 25$) | | CC ($n = 31$) | | OS ($n = 31$) | |
|------------|-------------------|------|------------------------|-------|------------------------|-------|------------------------|-------|------------------------|-------|
| | | | Model | r^2 | Model | r^2 | Model | r^2 | Model | r^2 |
| ln(BG) | ln(DBH) | 1991 | $1.71 \times a - 3.21$ | 0.65 | $1.99 \times a - 4.29$ | 0.94 | $1.80 \times a - 3.86$ | 0.77 | $1.86 \times a - 4.09$ | 0.84 |
| | | 1992 | $1.86 \times a - 3.86$ | 0.90 | $1.94 \times a - 4.09$ | 0.94 | $2.06 \times a - 4.55$ | 0.81 | $1.89 \times a - 4.15$ | 0.88 |
| | | 1993 | $1.84 \times a - 3.77$ | 0.88 | $1.88 \times a - 3.96$ | 0.90 | $1.58 \times a - 3.15$ | 0.83 | $1.80 \times a - 3.79$ | 0.90 |
| | | 1994 | $1.95 \times a - 4.14$ | 0.90 | $1.90 \times a - 4.02$ | 0.90 | $1.65 \times a - 3.36$ | 0.77 | $1.85 \times a - 3.97$ | 0.87 |
| | | 1995 | $1.96 \times a - 4.24$ | 0.83 | $1.91 \times a - 4.01$ | 0.89 | $1.47 \times a - 2.90$ | 0.77 | $1.82 \times a - 3.94$ | 0.90 |
| | | 1996 | $1.91 \times a - 3.92$ | 0.84 | $1.89 \times a - 4.00$ | 0.88 | $1.56 \times a - 3.19$ | 0.67 | $1.71 \times a - 3.65$ | 0.86 |
| | | 1997 | $1.98 \times a - 4.26$ | 0.87 | $1.77 \times a - 3.59$ | 0.86 | $1.58 \times a - 3.17$ | 0.77 | $1.83 \times a - 3.95$ | 0.90 |
| | | 1998 | $1.87 \times a - 3.76$ | 0.80 | $1.78 \times a - 3.66$ | 0.85 | $1.56 \times a - 3.08$ | 0.79 | $1.90 \times a - 4.08$ | 0.92 |
| | | 1999 | $1.91 \times a - 3.88$ | 0.85 | $1.79 \times a - 3.64$ | 0.85 | $1.61 \times a - 3.06$ | 0.77 | $1.80 \times a - 3.66$ | 0.88 |
| | | 2000 | $1.89 \times a - 3.87$ | 0.79 | $1.72 \times a - 3.43$ | 0.87 | $1.51 \times a - 2.89$ | 0.75 | $1.59 \times a - 3.24$ | 0.82 |
| | | 2001 | $1.85 \times a - 4.10$ | 0.86 | $1.63 \times a - 3.15$ | 0.88 | $1.45 \times a - 3.22$ | 0.73 | $1.41 \times a - 3.15$ | 0.78 |
| | | 2002 | $1.91 \times a - 3.99$ | 0.77 | $1.63 \times a - 3.15$ | 0.88 | $1.44 \times a - 2.64$ | 0.66 | $1.60 \times a - 3.08$ | 0.81 |
| | | 2003 | $1.78 \times a - 3.50$ | 0.77 | $1.57 \times a - 2.93$ | 0.82 | $1.82 \times a - 3.59$ | 0.71 | $1.55 \times a - 2.89$ | 0.79 |
| | | 2004 | $1.84 \times a - 3.78$ | 0.78 | $1.64 \times a - 3.13$ | 0.84 | $1.84 \times a - 3.68$ | 0.81 | $1.38 \times a - 2.39$ | 0.78 |

The models were derived from the regressions between DBH of 2005 in the uncored individuals and the wood biomass growth data from 1991 to 2004 in the cored individuals

Table 4 Summary of wood biomass production (WBP, $\text{g C m}^{-2} \text{ year}^{-1}$) in the study plots during 1991–2004

| Plot no. | Year | | | | | | | | | | | | | | | Plot-WBP |
|----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|----------|
| | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | | |
| 1 | 177.2 | 196.9 | 172.3 | 177.1 | 183.9 | 179.6 | 206.6 | 182.0 | 195.4 | 183.3 | 155.6 | 193.8 | 193.7 | 177.5 | 183.9 | |
| 2 | 220.8 | 208.8 | 231.8 | 215.5 | 211.3 | 221.9 | 227.0 | 228.5 | 241.3 | 230.3 | 161.2 | 241.6 | 248.0 | 252.4 | 224.3 | |
| 3 | 341.8 | 343.9 | 329.1 | 357.5 | 325.5 | 352.8 | 347.2 | 381.3 | 385.6 | 362.0 | 259.1 | 366.2 | 373.6 | 340.8 | 347.6 | |
| 4 | 321.6 | 337.0 | 372.4 | 332.0 | 369.8 | 392.7 | 376.7 | 372.0 | 413.1 | 374.5 | 238.1 | 331.6 | 319.3 | 337.9 | 349.2 | |
| 5 | 343.2 | 296.8 | 242.0 | 300.2 | 328.3 | 343.8 | 278.2 | 324.9 | 310.7 | 362.7 | 200.7 | 370.8 | 332.9 | 309.0 | 310.3 | |
| 6 | 119.4 | 131.3 | 125.6 | 137.3 | 129.4 | 132.9 | 131.4 | 108.6 | 139.6 | 122.2 | 84.4 | 113.1 | 139.2 | 139.6 | 125.3 | |
| 7 | 338.5 | 313.3 | 297.8 | 373.7 | 387.4 | 368.8 | 333.9 | 378.7 | 352.9 | 359.0 | 229.5 | 344.6 | 347.3 | 337.5 | 340.2 | |
| 8 | 134.8 | 140.8 | 152.1 | 140.7 | 130.3 | 145.1 | 161.4 | 170.3 | 188.8 | 171.5 | 129.8 | 185.6 | 212.8 | 181.9 | 160.4 | |
| 9 | 336.3 | 322.6 | 323.9 | 282.6 | 250.6 | 321.3 | 278.9 | 378.6 | 437.1 | 382.8 | 208.7 | 393.2 | 399.4 | 419.7 | 338.3 | |
| 10 | 331.0 | 344.1 | 339.8 | 326.5 | 319.1 | 327.3 | 349.3 | 352.0 | 382.9 | 324.3 | 220.2 | 356.1 | 370.7 | 338.2 | 334.4 | |
| Year-WBP | 266.5 | 263.6 | 258.7 | 264.3 | 263.6 | 278.6 | 269.1 | 287.7 | 304.7 | 287.3 | 188.7 | 289.7 | 293.7 | 283.5 | 271.4 | |

Plot-WBP and Year-WBP indicate 14-year mean WBP of each plot and 10-plot mean WBP of each year, respectively

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