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Regional scale variation in forest structure and arborous layer aboveground biomass along altitudinal gradient in the Qinling Mountains

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With the decrease of forest area and increase of greenhouse gases like CO₂, it is increasingly important to estimate forest biomass and carbon storage. For a better assessment of the variation of regional forest structure and arborous layer biomass at different altitudes in Qinling forest area, we studied the environment factors and interference factors of local forest, on the 50 selective sampling plots (800 to 2300 m). The results showed that low altitude forest was more severely disturbed by human being, with its structure different from other altitudes. The arborous layer biomass was between 104.76 ± 8.97 and 40.48 ± 3.03 mg ha⁻¹, negatively related to altitude ($r_p = -0.456$, $P < 0.05$), and positively related to age ($r_p = 0.596$, $P < 0.05$) and basal area ($r_p = 0.667$, $P < 0.01$). The temperature change related to altitudes and decreasing stem density were the main factors influencing forest stand biomass and productivity. The average individual biomass of broadleaved species decreased with increasing altitude, while that of coniferous species increased gradually, with some exception in low-altitude areas. The results showed that the forest biomass estimation in regional scale is different from that for larger scales. We must take into consideration inference factors and environment changes.

Key words: Arborous layer aboveground biomass, carbon pool, secondary mixed forest.

INTRODUCTION

The forest ecosystem contains 85 to 90% of carbon storage of terrestrial ecosystems (Whittaker and Likens, 1973), with its carbon storage easily influenced by logging, land utilization, climate change and other interference factors (Canadell et al., 2007). Mount Qinling, as the important ecological shelter zone in the Northeastern China, contains rich forest resources and carbon storage, and plays an important role in responding to regional climate change caused by CO₂ emission. However, the predatory logging in the past decades had severely decreased carbon storage in this area (Wang and Tan,

2011). Studying its forest biomass cannot only give us more understanding of forest dynamics, but also supply basic data for further studies of carbon storage and carbon cycling.

Aboveground biomass (AGB), as basic property of forest ecosystem, reflects forest management and production of a region. However, how to supply an accurate assessment of forest biomass is now the biggest problem facing ecologists and decision makers (Adrien et al., 2011). Recently, some researches tried to estimate AGB through forest inventory data (FID) in big scales (Brown, 1997), but for small scales this method can poorly work (Brown et al., 1989). Some tried to assess the spatial variation of AGB through remote sensing, but its accuracy needs calibration by data from sampling field (Houghton, 2005). In studying biomass of arborous layer,

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Table 1. Characterization of stand site at five altitudinal gradients of regional secondary mixed forest in Foping.

Site parameter	Forest type (dominant species)				
	<i>Pinus tabulaeformis</i> , <i>Quercus variabilis</i>	<i>Pinus tabulaeformis</i> , <i>Quercus</i> <i>aliena</i> var. <i>acuteserrata</i>	<i>Pinus tabulaeformis</i> , <i>Pinus armandii</i> , <i>Quercus aliena</i> var. <i>acuteserrata</i>	<i>Pinus armandii</i> , <i>Picea</i> spp., <i>Betula</i> spp.	<i>Betula</i> spp., <i>Larix</i> spp., <i>Picea</i> spp.
Altitudinal gradient	Low elevation (LE)	Mid-low elevation (MLE)	Middle elevation (ME)	Mid-high elevation (MHE)	High elevation (HE)
Sample plot number	10	10	10	10	10
Total area (ha)	0.6	0.6	0.6	0.6	0.6
Elevation (m/a.s.l)	800-1100	1100-1400	1400-1700	1700-2000	2000-2300
Topography	28.9-36.3°	24.3-31.4°	28.4-34.8°	27.4-38.2°	27.1-34.3°
Soil type	Yellow brown soil	Yellow brown soil	Brown soil	Brown soil	Brown soil

the choice of method depends on individual forest in individual area due to the variety in forest community (Feng et al., 1999). Thus, the dominant species allometric equation is still an important approach to evaluating regional biomass storage (Houghton et al., 2001). With influence of regional microclimate, forest structure and biomass vary with altitude gradient. Variation of altitude gradient mainly shows in that of temperature, solar radiation and atmospheric pressure (Korner, 2007). Other environment factors, like soil humidity, temperature and soil fertility, depend more on topography (Daws et al., 2002). Thus, forest structure and biomass are in different formation with different altitude gradients. AGB differs with stem distribution, soil fertility, topography and other interfering factors. Altitude gradient as one of the important influencing factors to mountain forest community and biodiversity plays an important role in revealing variation of plant community and that of biomass change with altitude.

This study aimed at using forest structure, interference factors and AGB, to explore the biomass variation in the south slope secondary forest in its primary stage of natural succession. The objectives of this research included: 1) to analyze the spatial distribution of forest structure

and AGB with relation to altitude gradients; 2) to assess the natural and human-caused interference factors to forest structure and AGB; 3) to compare the biomass and gross primary productivity (GPP) variation of coniferous and broadleaved species and 4) to forecast the successional process of this region so as to provide reference for operation planning.

MATERIALS AND METHODS

Study site and sample procedure

The study area (33°16'-33°45'N; 107°41'-108°10'E) is located at Changjiaoba, Foping County, Shaanxi Province, China. About 200 km from Xi'an to the north and 140 km from Hanzhong to its south, it is at the middle of the south slope of Mount Qinling. Foping is in the transitional zone of north subtropical and the warm temperate zones, with subtropical monsoon climate and typical mountain forest microclimate characteristics. Its main plant types are broadleaved deciduous and coniferous forests, as well as abundant scrubs, herbs and lianas (Dai et al., 2010). The area has an annual average temperature of 11.5°C, annual precipitation of 938.1 mm and annual average evaporation capacity of 1086.3 mm. Its soil presents as transition from low mountains to subalpine zones, namely yellow brown soil (< 1300 m) and brown soil (1300 to 2500 m). Species with most communities were Pinaceae, Taxodiaceae, Fagaceae, Betulaceae, and Aceraceae, etc. (Yue et al.,

1999). Among them, the dominant species are *Pinus tabulaeformis*, *Quercus variabilis*, *Quercus aliena* var. *acuteserrata*, *P. armandii*, *Larix* spp., and *Picea* spp., etc. Particularly, except for some steep area of high altitude, the plant of the research area was destroyed to different degrees by people in the late 1990's.

In general, our study area has forest coverage of over 85%, an important area for regional carbon balancing and stabilization. However, few studies were done in this area for forest structure, biomass, carbon storage, especially with relation to altitude dynamics. So, we chose 50 secondary mixed forests (30 m × 20 m, II – III site classes) as our sampling field at five altitude gradients (800 to 2300 m) at Changjiaoba, Foping County. Each gradient was 300 m away from another, to represent spatial variation of the forests (Table 1). The sample plots, all secondary coniferous-broadleaved mixed forest of similar environment factors, were each constituted of two or more species, with the ratio of conifer to broadleaved trees no less than 1:5 (Liu et al., 2010). In terms of species, the coniferous-broadleaved mixed forest was mainly characterized with *Quercus* spp. and *Betula* spp. as pioneer species, and *P. tabulaeformis*, *P. armandii*, *Larix* spp. as climax species. The age of forest was calculated with weighted averaging two or three trees of dominant species. The individual tree age was recorded by counting annual ring after using increment borer to drill into the pith of trees. The mixed forests were usually 30 – 50 years old, only three sampling plots older than 50. All trees with diameter at breast height (DBH) ≥ 5 cm were measured. In forests of small crown density, we measured the height of individual trees, but the result was not accurate enough for trees of great crown density (Gower et al., 1999). For such cases, we estimated

the height by the conventional yield table of individual species, or by DBH-height curve equation (Luciana et al., 2010).

Height-diameter model

The allometric equation $B = a (\text{DBH}^2 \times H)^b$ (Niklas, 1994), reflected the non-linear regression relations between the component biomass (the dependent variant) and the tree height (H) or DBH (the independent variants). In the equation, B is the biomass of each group. Because H was more difficult to measure than DBH in forests of high crown density, we used only DBH as the independent variant to calculate the AGB of each species, for more accuracy and convenience. The tree height was simply calculated with the growth process table of each dominant species at Qinling area, as well as the simulated DBH-H model. The relations between tree height and DBH are often expressed by non-linear mathematic models, most often in forestry study are: Chapman-Richards (Chapman, 1961; Richards, 1959), Weibull (Yang et al., 1978), Schnute (Schnute, 1981), Exponential (Ratkowsky, 1990), Logistic (Ratkowsky and Reedy, 1986) and Korf (Zeide, 1989). Among them Chapman-Richards model is good at reflecting biological properties of the trees, with effective predetermination. Based on previous studies, we adopted the Chapman-Richards function to fit H against DBH. The model form is:

$$H = 1.3 + a (1 - e^{-b \times \text{DBH}^c})$$

Where a , b and c are regression coefficients (Peng et al., 2001). And the PROC GLM procedure in SAS software version 9.0 was used for all analyses.

Analysis of forest structure

Through investigation on the sampling sites, we found out that the study area was rich in trees of small DBH. For better assessment of the altitude variation of the forest structure, we calculated based on the investigation results the following data: total tree stem density (DBH ≥ 5 cm and ≥ 10 cm), individual density classified by DBH, total arborous layer AGB, AGB of different DBH, as well as the basal area (BA) for forests at all altitudinal gradients (Luciana, 2010). We analyzed the response of forest structure to altitude gradients through the relations among forest biomass, GPP and forest stand factors.

Allometric equations to estimate AGB

To assess AGB on regional scale, we needed to consider the influences of environmental factors, species constitution and species structure (Brown, 1997). There were in previous studies some models for our reference (Table 2) on the allometric equations for the ecosystem of warm temperate zone and the dominant species in the Qinling area (Chen, 1984; Bao et al., 1984; Jiang, 1992; Cheng et al., 2007). These equations were suitable for AGB estimation when DBH ≥ 5 cm. For the forest reservation policies, we did not undertake destructive sampling.

Statistical analysis of AGB and GPP

For individual trees, we first calculated the biomass of each organ, and then added up as the individual biomass. The sampling sites were calculated for biomass in terms of coniferous and broadleaved species (Liu et al., 2010). The sum of these two species made the total biomass of the tree layer. Now we could derive forest biomass of unit area. The net primary productivity (ΔP_n) was the sum of

productivity (Y_n), mortality of litters (ΔL_n), and loss capacity that was eaten by animals (ΔG_n) (Ogawa and Kira, 1977). Only the average annual gross primary productivity of arborous layer was considered in this research. The gross primary productivity was calculated as follows:

$$\Delta P_g = W/a \quad (1)$$

Where ΔP_g is the productivity, W is the biomass of some forest age; and a is the forest age. The average individual biomass and productivity was also calculated as follows:

$$W_i = \frac{1}{mn} \sum_{j=1}^m \sum_{i=1}^n (W_{si} + W_{bi} + W_{li}) \quad (2)$$

Average individual productivity was also calculated as:

$$S_i = \frac{1}{mn} \sum_{j=1}^m \sum_{i=1}^n (s_i) \quad (3)$$

Where W_s , W_b , W_l stand for the biomass of stem, branch and leaf, respectively; S_i is the average individual productivity, s_i is the productivity of tree no. i ; m is the number of sampling sites at certain altitude gradient; n is the number of trees in certain sampling site. One-way analysis of variance was used to compare the difference of component biomass and GPP among five gradients, and partial correlation analysis was used to indicate relevance between stand biomass and forest factor.

RESULTS

Coefficients fitting of H-DBH model

The adapted form of Chapman-Richards function relating H to DBH provides a good fit for the allometric data (Table 3). This function was further plugged into the allometric equations (Table 2) to estimate biomass. For other broad-leaved trees, because of their various species and growth condition, we directly used allometric equations to calculate their biomass, instead of simulating individual height and DBH.

Forest structure variation

The variation of stem density, AGB and BA showed a decreasing trend with the increase of altitude gradient, except for low altitudes (Table 4). The estimated AGB and BA were greatest at the Mid-low elevation (MLE) gradient; at Low elevation (LE) gradient, the stem density was the biggest, while AGB and BA comparatively smaller. The other indexes all showed a decreasing trend with increasing altitude (Table 4). For arborous layer of DBH ≥ 5 cm, AGB decreased from 104.76 mg ha⁻¹ (95% CI: 76.21, 133.31) at MLE to 40.48 mg ha⁻¹ (95%CI: 30.83, 50.14) at High elevation (HE) gradient. BA decreased from 28.99 m² ha⁻¹ (95% CI: 24.21, 33.76) at MLE gradient to 12.01 m² ha⁻¹ (95% CI: 8.12, 15.91) at HE gradient. Trees with DBH ≥ 10 cm also showed the same rule, except in

Table 2. Allometric equations used to estimate stem AGB (mg ha⁻¹) at five sites along altitudinal gradients of regional secondary mixed forest in Foping.

Species	Allometric equation	Applicable range (DBH/cm)	Source
<i>Pinus tabulaeformis</i>	$W_s = \exp(-3.8828 + 0.9359\ln(\text{DBH}^2 \times H))$ $W_b = \exp(-6.3807 + 1.1242\ln(\text{DBH}^2 \times H))$ $W_l = \exp(-5.3277 + 0.8812\ln(\text{DBH}^2 \times H))$	2.8 ~ 22.5	Cheng et al. (2007)
<i>Pinus armandii</i>	$W_s = 0.01308(\text{DBH}^2 \times H)^{1.0038}$ $W_b = 0.0055(\text{DBH}^2 \times H)^{1.0439}$ $W_l = 0.0011(\text{DBH}^2 \times H)^{1.12566}$	4.0 ~ 36.0	Chen (1984)
<i>Larix</i> spp.	$W_s = \exp(-3.6844 + 0.9303\ln(\text{DBH}^2 \times H))$ $W_b = \exp(-7.6840 + 1.2554\ln(\text{DBH}^2 \times H))$ $W_l = \exp(-12.0638 + 1.4968\ln(\text{DBH}^2 \times H))$	1.7 ~ 21.0	Cheng et al. (2007)
<i>Picea</i> spp.	$W_s = \exp(-3.9744 + 0.9434\ln(\text{DBH}^2 \times H))$ $W_b = \exp(-4.6350 + 0.9257\ln(\text{DBH}^2 \times H))$ $W_l = \exp(-5.9391 + 0.9753\ln(\text{DBH}^2 \times H))$	4.6 ~ 25.0	Cheng et al. (2007)
<i>Quercus variabilis</i>	$W_s = 0.05012(\text{DBH}^2 \times H)^{0.92}$ $W_b = 0.0199(\text{DBH}^2 \times H)^{0.98}$ $W_l = 0.00295(\text{DBH}^2 \times H)^{0.75}$	3.0 ~ 21.0	Bao et al. (1984)
<i>Q. aliena</i> var. <i>acuteserrata</i>	$W_s = \exp(-4.0347 + 0.9953\ln(\text{DBH}^2 \times H))$ $W_b = \exp(-8.4741 + 1.3674\ln(\text{DBH}^2 \times H))$ $W_l = \exp(-8.4170 + 1.0888\ln(\text{DBH}^2 \times H))$	3.8 ~ 47.7	Cheng et al. (2007)
<i>Betula</i> spp.	$W_s = 0.14114(\text{DBH}^2 \times H)^{0.7234}$ $W_b = 0.00724(\text{DBH}^2 \times H)^{1.0225}$ $W_l = 0.01513(\text{DBH}^2 \times H)^{0.8085}$	2.0 ~ 26.0	Jiang (1992)
Other hardwoods species	$W_s = \exp(-3.8852 + 0.9803\ln(\text{DBH}^2 \times H))$ $W_b = \exp(-5.6360 + 1.0851\ln(\text{DBH}^2 \times H))$ $W_l = \exp(-4.5320 + 0.7377\ln(\text{DBH}^2 \times H))$	3.8 ~ 43.1	Cheng et al. (2007)

DBH: diameter at breast height, H: total tree height.

Table 3. Relationship between tree height (H/m) and diameter at breast height (DBH/cm) by different species.

Tree species	a	b	c	R ²	MSE	P-value
<i>Pinus tabulaeformis</i>	25.196	0.029	0.866	0.944	0.659	<0.0001
<i>Pinus armandii</i>	31.335	0.017	0.810	0.961	0.341	<0.0001
<i>Larix</i> spp.	25.249	0.048	1.174	0.958	0.311	<0.0001
<i>Picea</i> spp.	27.528	0.041	1.295	0.976	0.299	<0.0001
<i>Quercus variabilis</i>	14.063	0.081	1.118	0.862	0.576	<0.0001
<i>Quercus aliena</i> var. <i>acuteserrata</i>	19.569	0.020	0.564	0.821	1.201	<0.0001
<i>Betula</i> spp.	18.249	0.078	0.951	0.935	0.886	<0.0001

The regression coefficients of the model $H = 1.3 + a(1 - e^{-b \times \text{DBH}^c})$. Adjusted determination coefficient (R²) and mean square error (MSE) are given.

low altitudes.

With the increase of altitude gradient, stem density and AGB for different diameter classes varied greatly, with the

stem density showing a decrease trend. For each altitude gradient, there were scarce trees of big diameter (DBH ≥ 30 cm), but their proportion increased with altitude

Table 4. Stem density, stocks of AGB and BA of arborous layer along altitudinal gradient in study site.

Altitudinal gradient	Stem density (ha ⁻¹)	Biomass (Mg ha ⁻¹)	BA (m ² ha ⁻¹)
DBH ≥5 cm			
Low elevation (LE)	2018 (1389, 2645)	71.46 (52.33, 90.6)	19.76 (14.78, 24.74)
Mid-low elevation (MLE)	1806 (1619, 1990)	104.76 (76.21, 133.31)	28.99 (24.21, 33.76)
Middle elevation (ME)	1670 (1437, 1904)	71.25 (42.28, 100.22)	20.97 (13.74, 28.21)
Mid-high elevation (MHE)	1604 (1478, 1730)	53.84 (19.01, 88.67)	16.02 (8.67, 23.36)
High elevation (HE)	1367 (1185, 1548)	40.48 (30.83, 50.14)	12.01 (8.12, 15.91)
DBH ≥ 10 cm			
Low elevation (LE)	800 (722, 878)	40.79 (11.63, 87.18)	15.09 (10.42, 19.77)
Mid-low elevation (MLE)	887 (821, 954)	97.93 (70.26, 125.61)	26.16 (21.19, 31.14)
Middle elevation (ME)	760 (460, 1060)	64.38 (31.63, 97.14)	14.66 (7.75, 21.57)
Mid-high elevation (MHE)	658 (334, 983)	46.58 (10.34, 82.84)	12.82 (4.61, 21.04)
High elevation (HE)	496 (318, 675)	31.59 (19.43, 43.75)	8.73 (4.59, 12.87)

Values are means and bootstrapped 95% confidence intervals; n = 50.

(Figure 1A). Usually, the small diameter classes show bigger stem density but smaller biomass. However, the AGB (DBH<10 cm) were significantly higher ($P < 0.05$) at LE and MLE gradients than others, being 16.21 and 15.83 mg ha⁻¹, respectively. At Mid-high elevation (MHE) and HE gradients, trees of big diameter (> 20 cm) were scarce, but with comparatively big proportion of the AGB at 65.5 and 74.1%, respectively. At other gradients, AGB showed a big concentration in the middle, that was, $10 \leq \text{DBH} \leq 30$ cm; the proportions being 65.0% at LE, 69.5% at MLE, and 65.6% at Middle elevation (ME) gradients (Figure 1B).

Environmental and disturbance determinations of AGB

The partial correlation analysis on AGB, productivity and main forest stand factor showed a negative relation between altitude and stem density ($r_p = -0.771$, $P < 0.01$), tree layer biomass ($r_p = -0.456$, $P < 0.05$), and GPP ($r_p = -0.475$, $P < 0.05$). On the other hand, the forest age was positively related to forest basal area, tree layer biomass, and productivity, with r being 0.406, 0.596, 0.413 respectively, $P < 0.05$. The basal area was positively related to arborous layer biomass ($r_p = 0.667$, $P < 0.01$) and GPP ($r_p = 0.645$, $P < 0.01$). The altitude was to some degree positively related to the conifer-broadleaved ratio, but not significantly ($P > 0.05$), which meant more sensitive response of conifers to altitude gradient than the broadleaved species. Generally, the forest age and basal area had greater influence than the forest density on biomass productivity.

Forest BA in sapling forest ranged from 6.43 m² ha⁻¹ (17 years) to 18.27 m² ha⁻¹ (28 years) (11.08 ± 1.31 m² ha⁻¹, $n = 8$) in forest younger than 30 years. In forests of 30 to 50 years old, however, the basal area was between

9.53 and 30.74 m² ha⁻¹ (22.87 ± 1.44 m² ha⁻¹, $n = 37$). Forests older than 50 years were all over 1800 m in altitude. Moreover, due to less natural and human caused influence, their basal area was between 22.04 and 39.25 m² ha⁻¹ (32.57 ± 1.96 m² ha⁻¹, $n = 5$). The biomass was 39.99 ± 2.61 mg ha⁻¹ in the forests younger than 30 years, 80.48 ± 5.93 mg ha⁻¹ in the forests between of 30-50 years, and 106.10 ± 5.52 mg ha⁻¹ in the forests older than 50 years. All the differences among forests of different ages were statistically significant ($P < 0.01$). Both AGB and BA increased with forest age, presenting certain linear relation (Figure 2).

AGB of arborous layer along altitudinal gradient

With the estimated arborous layer AGB, we analyzed the biomass components of coniferous and broadleaved species in relation to altitudinal gradient. The biomass of arborous layer broadleaved-coniferous mixed forest at Changjiaoba, Foping County showed a significant declining trend ($P < 0.05$) at the increase of altitude with the forest total biomass decreasing from 104.764 ± 8.971 mg ha⁻¹ at MLE gradient to 40.485 ± 3.035 mg ha⁻¹ at the HE gradient (Table 5). Conifers and broadleaved species followed the same rule, with the highest biomass at MLE gradient, 52.998 ± 15.004 and 51.766 ± 14.832 mg ha⁻¹, respectively, then gradually decreased. The decrease was in greater degree in broadleaved species than in coniferous ones. The biomass ratio of stem, branch and leave kept stable in coniferous species, namely 63%:28%:9%.

In broadleaved species, however, the leave biomass increased in proportion with altitude, from 1.9% at LE to 10.2 at HE level. The proportion of other parts decreased at the same time, but not significantly (Table 5). With the increase of altitude, the broadleaved biomass accounted

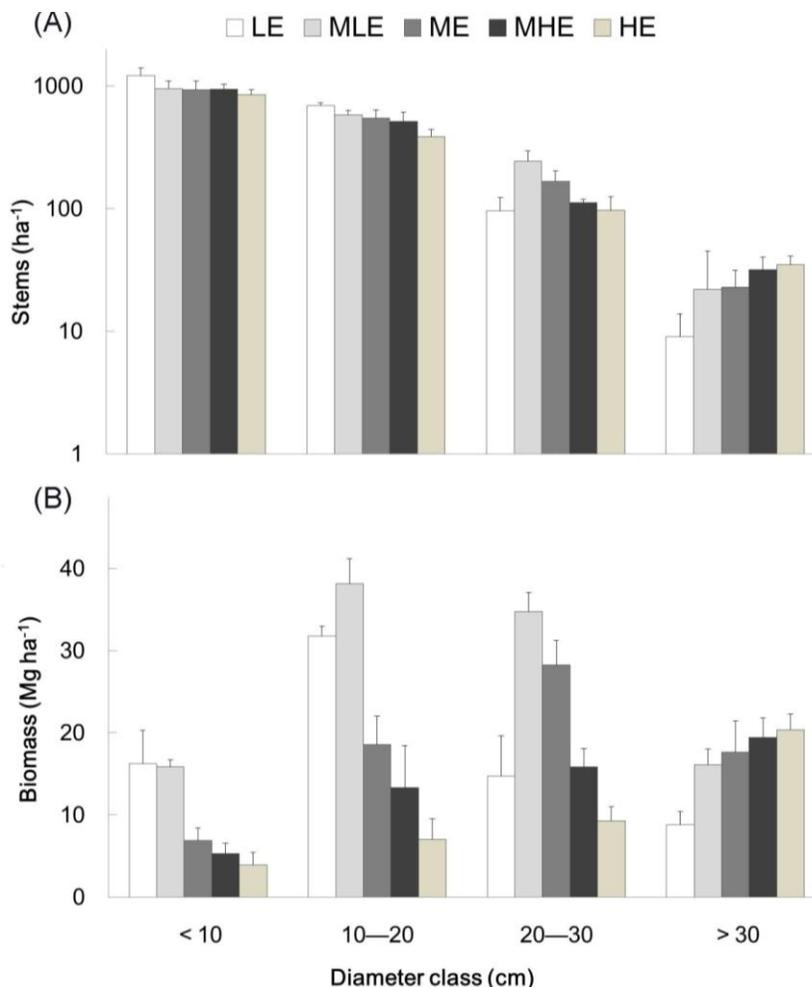


Figure 1. Distribution of numbers of stems (ha^{-1}) and biomass (Mg ha^{-1}) by diameter size class on different mixed forest along altitudinal gradient in study site. Values are means \pm S.E.; $n=50$.

for less and less proportion in forest arborous layer biomass. The dominant species changed from *Quercus* spp. and *Acer* spp. at lower altitude to climax species like *Picea asperata*.

Individual biomass of conifers and broadleaved species

The individual biomass could reflect individual difference and its response to altitude. With the increase in altitude, the average individual biomass (in the form of biomass components) of broadleaved trees kept decreasing (except in LE gradient) from 51.98 kg at MLE to 35.99 kg at HE gradient. On the other hand, the average individual biomass of conifers kept increasing, from 42.81 kg at LE to 56.42 kg at HE. At low altitude gradients, broadleaved species had bigger individual biomass than the conifers. But with the increase of altitude, conifers became bigger

in individual biomass. The higher the altitude, the more obvious the difference, which suggested that conifers were better adapted to habitat changes caused by altitudinal increase.

Similar to forest biomass components, the biomass of average individual stems and leaves became bigger with increase of altitude, while that of branches became smaller. Unlike the conifers, the broadleaved species had smaller biomass components at higher altitude (Figure 3), but its stem biomass kept stable, around 61%. The biomass components in conifers were about 64%:25%:11%, similar to that of biomass components of unit area of coniferous forests.

Aboveground gross primary productivity of coniferous-broadleaved forest

With increase of altitude, both forest productivity and

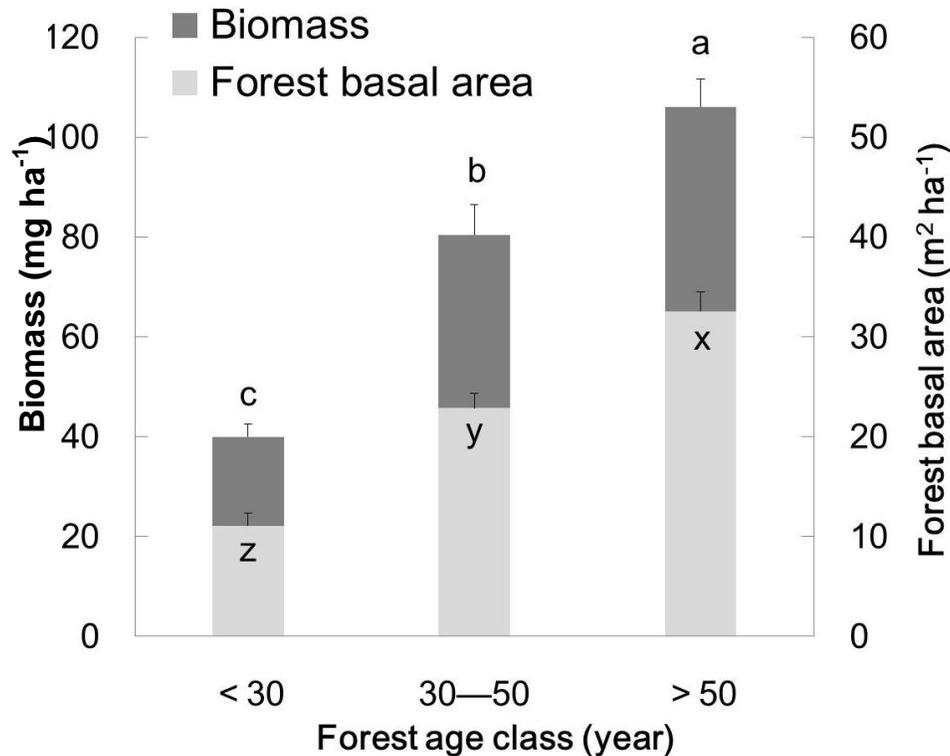


Figure 2. Mean AGB (Mg ha⁻¹) and forest basal area (m² ha⁻¹) for three classes of mixed forest in study site.

Table 5. Variation of arborous layer biomass and statistical test along altitudinal gradient.

Forest types	Altitudinal gradients (m)	Component biomass (mg ha ⁻¹)			
		Stem	Branches	Leaves	Total
Conifers	Low elevation	20.769 ± 4.020 ^a	8.083 ± 1.557 ^{ab}	3.137 ± 0.612 ^{ab}	31.989 ± 6.179 ^a
	Mid-low elevation	32.884 ± 9.416 ^a	15.280 ± 4.273 ^a	4.833 ± 1.322 ^a	52.998 ± 15.004 ^a
	Middle elevation	27.560 ± 4.315 ^a	13.377 ± 2.109 ^{ab}	4.865 ± 0.788 ^a	45.802 ± 7.076 ^a
	Mid-high elevation	18.228 ± 4.136 ^a	9.137 ± 2.801 ^{ab}	3.546 ± 1.104 ^{ab}	30.911 ± 8.025 ^a
	High elevation	17.417 ± 3.312 ^a	6.826 ± 0.454 ^b	2.463 ± 0.389 ^b	26.706 ± 3.224 ^a
	F-statistic	1.298	2.314	2.446	1.629
Broadleaved	Low elevation	25.001 ± 6.294 ^{ab}	13.687 ± 3.018 ^a	0.785 ± 0.340 ^c	39.473 ± 9.624 ^{ab}
	Mid-low elevation	35.673 ± 9.714 ^a	13.992 ± 5.517 ^a	2.102 ± 0.488 ^a	51.766 ± 14.832 ^a
	Middle elevation	16.997 ± 2.856 ^{ab}	6.530 ± 1.613 ^a	1.922 ± 0.799 ^{ab}	25.452 ± 4.879 ^{ab}
	Mid-high elevation	15.102 ± 5.901 ^{ab}	5.960 ± 2.727 ^a	1.868 ± 0.365 ^{bc}	22.930 ± 9.945 ^{ab}
	High elevation	7.513 ± 1.854 ^b	4.862 ± 0.447 ^a	1.404 ± 0.289 ^{bc}	13.779 ± 2.838 ^b
	F-statistic	2.613	1.781	3.553*	2.157
Total biomass	Low elevation	45.771 ± 3.949 ^b	21.770 ± 2.048 ^{ab}	3.922 ± 0.435 ^b	71.462 ± 6.013 ^b
	Mid-low elevation	68.558 ± 5.368 ^a	29.272 ± 3.260 ^a	6.934 ± 0.981 ^a	104.764 ± 8.971 ^a
	Middle elevation	44.560 ± 6.091 ^b	19.907 ± 3.372 ^{abc}	6.787 ± 1.156 ^a	71.253 ± 10.434 ^b
	Mid-high elevation	33.329 ± 6.339 ^{bc}	15.797 ± 3.965 ^{bc}	4.714 ± 0.998 ^{ab}	53.84 ± 10.945 ^{bc}
	High elevation	26.930 ± 2.889 ^c	10.688 ± 0.786 ^c	2.867 ± 0.363 ^b	40.485 ± 3.035 ^c
	F-statistic	8.716**	5.115**	5.185*	7.284**

Mean ± S.E.; n = 50; each gradient that shared a same letter were not different significantly ($P > 0.05$), while different letter were significantly different ($P < 0.05$). * $P < 0.05$; ** $P < 0.01$.

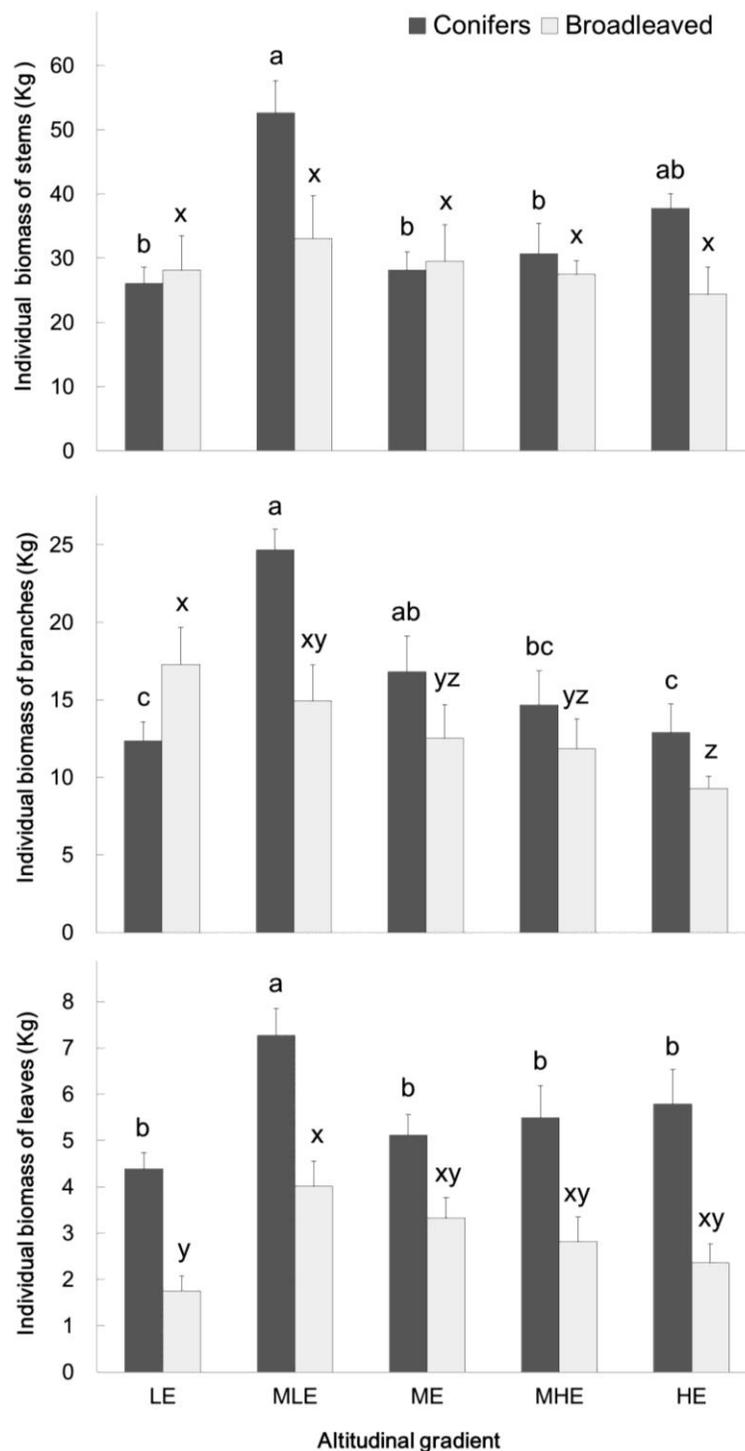


Figure 3. Mean individual biomass (\pm S.E.) for components of different species across altitude. Comparisons, indicated with superscripts, are based on a multiple comparison of mean test, with a and b indicating significant differences for conifers, and x, y and z for broadleaved species.

individual productivity decreased (except at the LE gradient, Figure 4A), from 3.351 and 3.345 $\text{mg ha}^{-1} \text{year}^{-1}$, respectively, at the MLE to 1.989 and 2.285 $\text{mg ha}^{-1} \text{year}^{-1}$

at the HE gradient. At altitudes less than 1100 m per unit area, productivity was higher in broadleaved than in coniferous species. For altitudes higher than 1100 m, the

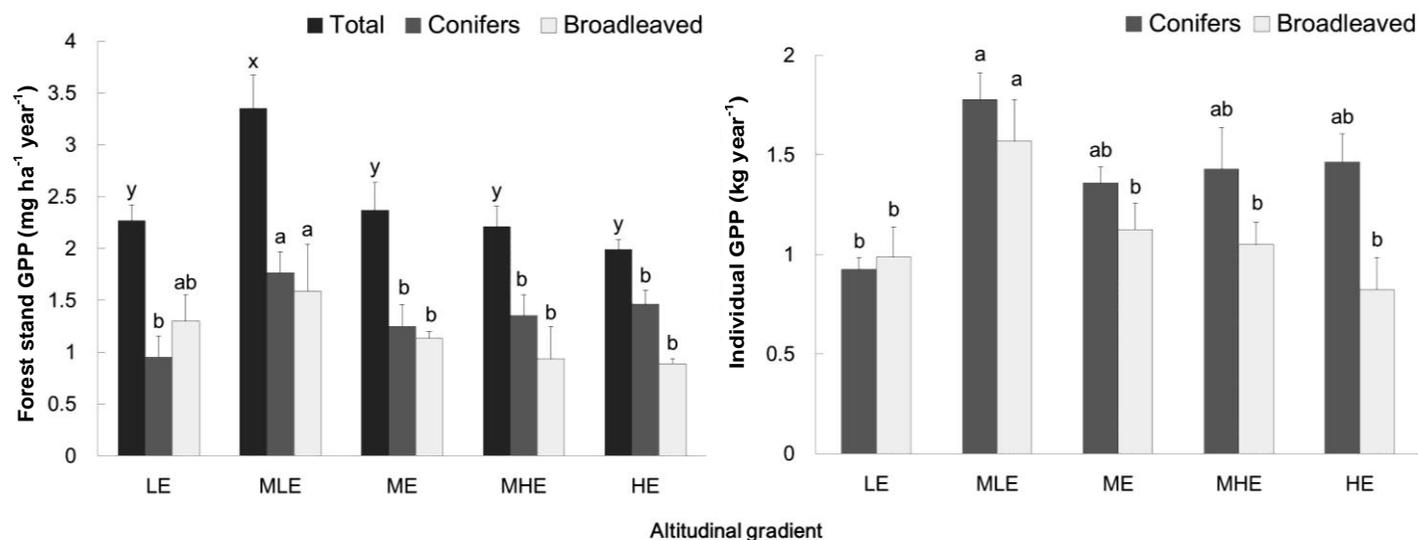


Figure 4. Mean forest stand and individual GPP (\pm S.E.) for different species along altitude. The superscripts with a and b indicate significant different for different species, while x and y for total GPP.

contrary was true.

In general, the coniferous and broadleaved species showed opposite variation trends in average individual productivity (Figure 4B). With the increase in altitude, the average individual productivity of broadleaved species kept decreasing from $1.507 \text{ kg year}^{-1}$ at the MLE gradient to $0.822 \text{ kg year}^{-1}$ at the HE gradient; but that for the coniferous species kept rising from $0.925 \text{ kg year}^{-1}$ at the LE level to $1.463 \text{ kg year}^{-1}$ at the HE level. At altitudes higher than 1100 m, the average individual productivity was higher in conifers than in broadleaves.

DISCUSSION

Effects of forest disturbance on DBH, stem density and BA

The diameter class distribution of a forest could reflect basic condition of its forest structure (Davis and Johnson, 1987). The stem density and BA per unit area could reflect the individual relation and spatial distribution. In our study, with the increase of altitude, stem density, AGB and basal area per unit area all decreased, both in forests of $\text{DBH} \geq 5 \text{ cm}$ and $\text{DBH} \geq 10 \text{ cm}$ (Table 4), suggesting a decreased utility of land resources by forests (Krebs, 1989). Because in general, the most important deciding factor of stem density and basal area was time of disturbance. If no severe disturbance, forests older than 30 years will keep increasing in both BA and AGB, so that many old forests have individuals with high AGB, like what we observed at the MHE and HE gradients in the present study. But with the decreased stem density at high altitudes, the general BA and AGB were in a lower level. That is to say, the spatial variation of biomass in

small area scale mainly depended on the disturbance factors (Chave et al., 2001). Also the forest age was positively related to AGB, with older forests having bigger AGB in this study (Figure 2).

Anthropogenic disturbance

Many researches show that the increase of altitude is often accompanied by decrease of biomass (Raich et al., 1997; Leuschner et al., 2007). But in this study, we found different models of biomass variation in relation to altitude change, namely an obvious small AGB at LE than MLE gradient (Table 4). We also observed in the LE gradient that there were more trees of small diameter ($\text{DBH} \leq 20 \text{ cm}$) than big diameters; and the proportion of biomass concentrated within 20 cm of the stem diameters. Forest biomass variation in big scales is often attributed to temperature and humidity, while that in small region scales is attributed to disturbance factors (Houghton, 2005). Human-caused disturbance is an important factor influencing forest structure variation and biomass accumulation (Clark, 2007). In our study area, the LE gradient (altitude 800 to 1100 m) was the main area of residency and agriculture, where people's using forest could account for the spatial variation of AGB in terms of altitude. At such low altitude plain area, human accessibility caused disturbance (Negrelle, 2002). The intensive small-diameter trees and relatively low biomass (Figure 1-B) at the low altitude areas (LE and MLE) could reflect the human disturbance and forest recovery course. In the high altitude areas, however, human disturbance was scarce, because of the steep and rugged paths. But with small stem density there, the AGB was comparatively small too.

Due to the disturbance of natural or anthropogenic, the big forest space could provide sufficient light with little competition (Hubbell et al., 1999), thus sapling distribution and growth was accelerated in these forests, especially with small crowns. In our investigation area, the majority of forests were replanted to ultimately recover the forest condition. The main replanted species were conifers. For these reasons, although the sampling sites were mainly natural secondary mixed forests, human interference and disturbance made coniferous biomass higher than broadleaved one at every altitude gradient (except for LE). At the MLE gradient, conifer biomass was bigger than higher altitude because this natural secondary conifer-broadleaved mix forest generated at the 1960s experienced little human destruction. Long term natural recovery made conifers its climax species. Other species, although rich in variety, their growth condition was poor, due to the poor condition of light, nutrition and competition (Figure 1). Thus, in these forests, conifer biomass became the dominant part of the whole forest.

AGB and GPP of mixed-forest along altitudinal gradient

Our investigation found that the arborous layer biomass of the coniferous-broadleaved mixed forests decreased with the increase of altitude. The lower altitude areas, however, did not follow this rule, because of human disturbances. The forest coniferous and broadleaved total biomass also decreased significantly ($P < 0.05$) with the increase of altitude. Besides, the forest arborous layer and individual productivity decreased. This was probably caused by the bad habitat condition at higher altitudes. The research area was located at the middle of south slope of Qinling Mountain. With every 100 m of altitude increase, the average temperature drops by 0.5 °C (Li et al., 2010). So the temperature difference between the LE and HE gradients was about 12.5 °C. In addition, in the high altitude area, the air was thin, the soil contained little water, the accumulated temperature was low. Under such poor climate condition, the plant growth cycle shortened, thus affecting organic synthesis in plants (Liu et al., 2006). In terms of biomass components, the proportion of stem and branch decreased with the increase of altitude, while that of the leaves kept increasing (Table 5, Figure 3). Such different variation trend of different parts of a plant was probably a kind of investigation strategy of community to make the biggest living space, so as to adapt better to the environment. The increase of leave biomass with the altitude intensified its assimilation, so as to accumulate organism to adapt the whole plant to critical growth environment.

The individual average biomass and productivity of broadleaved species decreased significantly ($P < 0.05$) with the increase of altitude. At high altitudes, the dominant broadleaved species was mainly *Betula* spp. Here, the forest general DBH was comparatively small,

with scarcely big diameters (DBH > 30 cm) (Figure 1). On the other hand, with higher altitude, coniferous species gradually became the dominant ones, with the community developed to the climax of succession. This is probably because of the strong cold resistance, sensitivity in humidity, and demand of winter precipitation of conifers (Li, 1997). With the increase of altitude, the temperature dropped, but precipitation and humidity increased, which was favorable to the growth of conifers. In addition, with the gradual decrease of forest density (Table 4), the internal competition weakened, providing more resources for coniferous species, thus increasing its individual productivity.

Uncertainties in estimating AGB

The stem density and height, two very important forecasting parameters in assessing forest biomass, vary with forest species constitution, forest type, age, and soil fertility (Chave et al., 2006). The sampling sites in our study were coniferous-broadleaved mixed forests, all about 40 years old, with similar soil type and fertility. They were the typical stem density in their respective altitude gradients. Unlike DBH, however, the height measuring caused some difficulty, especially in forests of high crown density, which formed one of the important uncertainties in AGB estimation. Another cause of uncertainty came from natural forest protection policies. The policies forbid destructive sampling, thus the AGB was not from accurate recording, but based on data from previous researches. If combined with remote sensing or other more complete studies on the area, our result could have had a higher accuracy. The further studies will try to focus on underwood biomass on a larger sampling area, so as to reach an accurate and objective evaluation of the biomass in this area.

Comparison of forest AGB with other neighboring regions in Qinling Mountains

There are presently very few studies about biomass at Qinling area, most of which are limited to forest carbon storage with FID or remote sensing. Combining the results of our present study and the few ones about allometric equations of dominant species (Chen et al., 1984; Ma, 1988; Cheng et al., 2007), we found that the secondary *P. tabulaeformis* forest at the LE altitude had a lower AGB (31.989 mg ha⁻¹) than its correspondence at the north slope of Mount Qinling (Mean AGB: 96.7 mg ha⁻¹) (Ma, 1988). The AGB of the secondary *P. tabulaeformis* forest at MLE (50.815 mg ha⁻¹) and the secondary *P. armandii* forest at the ME (43.041 mg ha⁻¹) gradient was lower than the corresponding forests at the north slope of Mount Qinling and the Qinling forest (62.02 mg ha⁻¹) (Chen, 1984). The AGB of secondary *Picea* spp. Forest (approximately 41.657 mg ha⁻¹) and *Larix* spp. forests

(25.471 mg ha⁻¹) were also lower than the same forest types at the Xiaolongshan area (75.313 and 49.257 mg ha⁻¹, respectively). In terms of the whole Mount Qinling area, its coniferous-broadleaved mixed forests had greatly lower biomass than the average (Feng et al., 1999).

Conclusion

This study made a primary estimation of the arborous layer biomass of the coniferous-broadleaved mixed forests with data from field investigation. We also analyzed the forest structure variation in relation to altitude gradient. The study area was found out to be in a primary stage of natural succession due to the human disturbance, including previous destructive logging, later forest thinning and replanting measures. The Mount Qinling is rich in precipitation, so temperature becomes the main influencing factor to plant growth. Driven by the global warming, plant community is gradually moving to higher altitudes. So we have reason to believe that the biomass of all gradients will increase in different degrees. The higher the altitude, the more obvious such increase. Thus, the forest environment at higher altitudes will assimilate to the lower ones. With rapid increase of biomass at high altitudes, the difference between high and low altitudes is likely to gradually decrease.

Moreover, in terms of forest management, analyzing the forest structure and AGB is important for future management decision making. Unlike the previous focus on community classification and variety studies, we need to establish long-term surveying sampling plots, to better evaluate growth variation and forest carbon storage with changes of climate and soil utilization. Given the present low forest biomass and carbon storage in this area, it is suggested that the local government take protective and management measures to attach priority to sustainable operation of forest, so as to achieve favorable carbon storage and carbon cycling.

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