The asynchronous response of carbon gain and water loss generate spatio-temporal pattern of WUE along elevation gradient in southwest China

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Abstract: The ratio of carbon gain to water loss, or water use efficiency (WUE), is a key characteristic of ecosystem function, and reflects the trade-off relationship between carbon gain and evapotranspiration (ET). The carbon and water cycles are very complex at the ecosystem scale, especially along altitudinal gradients. A stable carbon isotope method and the AVIM2 model were used to study the temporal and altitudinal patterns of carbon gain, water loss and ecosystem WUE in dark coniferous forests (Abies fabri) in subalpine, Southwest China. WUE was defined using different components of carbon gain and water loss. The temporal and altitudinal variations of WUE were found. WUE in the vegetative season was larger than in the dormant season. Climatic conditions such as monthly precipitation, air temperature, vapor pressure deficit (VPD) and net radiation contributed to the monthly variation in ecosystem WUE. Both the carbon gain and water loss decreased as the altitude increased, and the carbon gain exhibited a moderately decreasing rate compared with that of the water loss along the altitude gradient. WUE exhibited an increasing trend along the elevation gradient, but discrepancies appeared when different definitions of WUE were used. Variations in WUE indicated different coupling relationships between the carbon gain and water loss on different temporal and altitudinal scales. The asynchronous response of the carbon gain and water loss to climatic and physiological variables determined the temporal and altitudinal patterns of ecosystem WUE.

Keywords: Water use efficiency, dark coniferous forest, temporal, elevation, southwestern China
1. Introduction

The carbon and water cycles of terrestrial ecosystems are key ecological processes that are tightly coupled via the ecosystem water use efficiency (WUE, the mass ratio of CO₂ assimilated during photosynthesis to evaporated or transpired H₂O) (Yu GR et al., 2008; Beer et al., 2009; Keenan et al., 2013). The carbon and water cycles are very complex on the ecosystem scale, especially along altitudinal gradients, these cycles are influenced by variations in climate (Goulden et al., 2012) and plant physiology (Hultine and Maeshell, 2000; Li CY et al., 2009). The WUE is an important indicator of the coupled relationship between the carbon cycle and the water cycle (Alice et al., 2011). The variation of the δ¹³C in bulk leaf tissue has been described in southwestern China (Luo TX et al., 2005; Li CY et al., 2009; Li JZ et al., 2009), but the altitudinal and seasonal patterns of carbon gain and water loss are poorly understood.

Knowledge of WUE along altitude gradients is critical to understand the potential responses of trees to climate change. Farquhar et al. (1982, 1989) found that the stable carbon isotope composition of leaf tissue was related to $c/c_2$ and can therefore be used to calculate the intrinsic water use efficiency. Over the past several decades, δ¹³C has been widely used as an indicator of intrinsic WUE on different scales such as the leaf, plant and ecosystem scales (Bonal et al., 2000; Lauteri et al., 2004; Sauer et al., 2004; Ponton et al., 2006). Most studies have demonstrated that altitude has a positive effect on δ¹³C in the subalpine zone (Hultine and Marshall, 2000; Li et al., 2004; Li CY et al., 2009). Bert et al. (1997) found that WUE increased by 30% from the 1930s to the 1980s. In order to fully understand WUE along altitude, we still need to study different
response of carbon gain and water loss to environmental variables.

The seasonal patterns of WUE and its components reveal how mechanisms that lead to long-term and altitudinal WUE vary by plant functional type. WUE are controlled by environmental factors, such as the soil water content, atmospheric CO₂ concentration, air temperature, vapor pressure deficit and solar radiation, and physiological factors such as canopy conductance and nutrient content (Hultine and Maeshell, 2000; Li Chunyang et al., 2009; Goulden et al., 2012). Evapotranspiration (ET) accounts for up to 95% of the water loss from an ecosystem (Huxman et al., 2005). Recent studies have paid more attention to the seasonal variation of WUE with changes in the global climate (Yu GR et al., 2009; Keenan et al., 2013; Li SE et al., 2015). However, the responses of the carbon gain and water loss to climatic variables and canopy conductance depend on the forest types and even seasons. The temporal and altitudinal variations in ecosystem WUE are largely unexplained (Reichstein et al., 2014). Further research is needed to reveal the main influences and the response relationships among the carbon gain, water loss and environmental factors for different forest types.

Moreover, both the carbon gain and water loss consist of distinct components. For ecosystems, WUE is expressed as the ratio of net or gross ecosystem production to water loss (Law et al., 2002). However, the definitions and meanings of WUE expressed by different components of carbon gain and water loss were different (Yu GR et al., 2009; Hu ZM et al., 2010), or were only weakly correlated (Ito and Inatomi, 2012). Therefore, different definitions of WUE cannot be compared directly.
Abies is the dominant species in coniferous forests of the Northern Hemisphere (Wang et al., 2014). Most Abies are distributed over a broad vertical range in mountainous regions. Abies also form typical subalpine dark coniferous forests in southwestern China (Lv et al., 2009). The mountainous area in southwestern China is the source region of 6 main rivers and the second largest forest area in China (Sun HL, 2005; Wang GX et al., 2011). The subalpine coniferous forest is highly sensitive to climate change (Gao and Wang, 2007). Abies play an important role in the trade-off relationship between carbon storage and water resources. The temporal and altitudinal pattern of WUE in subalpine forests in southwestern China is still not characterized despite obvious practical importance. To address these questions, both model and stable isotope methods are adopted to simulate and elucidate the carbon gain, water loss and their components. The AVIM2 (Atmospheric-vegetation interaction model) was performed to simulate GPP, NPP, ET and its three components. The aim of this study is to 1) analyze the temporal and altitudinal pattern of the ecosystem WUE using a different definition for Abies fabri, 2) demonstrate why WUE of Abies fabri increased or decreased with altitude in the subalpine mountains.

2. **Materials and methods**

2.1. **Study area**

The study was conducted at Gongga Mountain (29°20′–30°20′ N, 101°30′–102°15′ E), which is located in the transitional area between the eastern monsoon subtropics of China and the frigid region of the Tibetan Plateau. It is the summit of Hengduan Mountain. The climate is dominated by the southeastern Pacific monsoon. The annual
mean air temperature in this region is 3.9 °C at an altitude of 3000 m, and the annual rainfall is 1940 mm, with most rainfall events occurring between May and October, which account for 79.7% of the annual rainfall. The relative humidity during the wet season is 91%. The annual mean air temperature decreased at a rate of 0.6 °C per 100 m along the altitudinal gradient.

The wide altitude range (1100–7556 m) results in a diverse range of vegetation zones, with forest types varying from subtropical to cold alpine vegetation. *A. fabri*, which is a part of the dark coniferous forest, is the dominant tree species in study area on the eastern slope of the Gongga Mountain from 2800 to 3700 m a.s.l (the alpine treeline). The dark coniferous forest is the zonal vegetation of the cold temperate zone and the widespread subalpine forest type in southwestern China and the northern hemisphere. The soil has developed from granite and is classified as a mountain gray-brown soil, which has a high sand content and strong permeability (He YR et al., 2005).

### 2.2. AVIM2 model

The GPP, NPP and ET were simulated using the Atmospheric-Vegetation Interaction Model (AVIM2) that was developed for simulating seasonal and interannual variations in biophysical and biogeochemical processes at the land surface. The AVIM2 includes a physical process module (PHY), a physiological plant growth module (PLT) and a soil carbon and nitrogen dynamics module (SOM).

#### 2.2.1 Physical process module

PHY is a typical soil vegetation atmosphere transfer scheme (SVAT), which is based on the work of Ji and Hu (1989), while for the new version of AVIM, snow
accumulation and snowmelt processes are added (Lu and Ji, 2006). The physical processes of PHY include the radiation transfer, the sensible and latent heat fluxes between the air, canopy and soil, the interception of rainfall and drainage, runoff and infiltration, transpiration from the canopy and evaporation from the surface, and snow accumulation and snowmelt processes. The components of ET consisted of canopy interception (Eint), transpiration (Et) from the canopy, evaporation from the soil (Es) and evaporation from snow cover. The other details of these processes are given by Ji and Hu (1989), Ji (1995) and Lu and Ji (2006).

2.2.2 Physiological plant growth module

The vegetation is separated into three components: the foliage, the fine roots and the remaining parts. Detailed descriptions of this process can be found in Ji et al (2005), Lu and Ji (2006) and Huang et al. (2007). When atmospheric CO2 enters through the stomata, dry matter is produced via photosynthesis. The gross primary production (GPP) is calculated based on the Farquhar model, which is based on the biochemistry of photosynthesis (Farquhar et al., 1980):

\[ \text{GPP} = \min(w_c, w_j) \]  

where \( w_c \) is the Rubisco-limited carboxylation rate, and \( w_j \) is the carboxylation rate limited by the rate of RuBP regeneration in the Calvin cycle. The carboxylation rate is a function of the environment temperature, leaf nitrogen concentration and leaf water potential.

The loss of dry matter is due to the respiration of the plant \( (R_t) \), which includes maintenance \( (R_m) \) and growth \( (R_g) \) components (Kozlowski, 1992).
\[ R_t = R_m + R_g = a \cdot BM + b \frac{dB M}{dt} \]  

(2)

where \( BM \) is the total living biomass, which is the sum of the foliage, fine roots and remaining parts, and \( t \) is the time step.

The residue of gross photosynthesis minus total respiration, which is named net primary productivity (NPP), is allocated to plant organs.

\[ NPP = A_c - R_m - R_g \]  

(3)

Then, the changing rates of biomass for leaves, stems and root are as follows:

\[ (1 + b) \frac{dM_f}{dt} = \alpha_f (A_c - R_m) - \mu_f M_f \]  

(4)

\[ (1 + b) \frac{dM_r}{dt} = \alpha_r (A_c - R_m) - \mu_r M_r \]  

(5)

\[ (1 + b) \frac{dM_s}{dt} = \alpha_s (A_c - R_m) - \mu_s M_s \]  

(6)

where \( M_f, M_s, M_r \) are the biomass of the leaves, stems and roots, respectively. The subscripts \( f, s \) and \( r \) denote the variables for leaves, stems and roots, respectively. \( \alpha_f, \alpha_r \) and \( \alpha_s \) are the allocating coefficients of assimilated matter, with \( \alpha_f + \alpha_r + \alpha_s = 1 \). \( \mu_f, \mu_r \) and \( \mu_s \) are the rates of litterfall.

2.2.3 Soil carbon and nitrogen dynamics module

The SOM simulates the transformation and decomposition of soil organic carbon and nitrogen mineralization. It was developed on the basis of soil carbon and nitrogen dynamics modules of CENTURY (Parton et al., 1987) and CEVSA (Cao and Woodward, 1998). The soil organic matter was divided into eight pools, i.e. surface structural and metabolic litter, structural and metabolic root litter, surface microbes and soil microbe, slow and passive carbon. The split of plant residue into metabolic \( (F_M) \) and structural components \( (F_S) \) are determined as a function of the lignin/nitrogen ratio (L/N), as
shown by the following equation (Parton et al., 1987):

\[ F_M = 0.85 - 0.018 \frac{L}{N} \quad (7) \]

\[ F_S = 1 - F_M \quad (8) \]

All carbon transformations between these eight pools and be decomposed of each pool is expressed as followed:

\[ \frac{dQ_i}{dt} = K_i f(T)f(W)Q_i + d_{ij}Q_j + F \quad (9) \]

Where \( Q_i \) is the carbon density of each pool, \( K_i \) is maximum decomposition rate, \( f(T), f(W) \) is the effect of soil temperature and moisture on decomposition rate, \( d_{ij} \) is the transformational rate between pools and \( F \) is the input of litter carbon.

The sum of gaseous carbon loss from various soil carbon pools caused by microbial decomposition is heterotrophic respiration (HR):

\[ HR = \sum_i Q_i K_i (1 - \varepsilon) \quad (10) \]

Where \( \varepsilon \) is the assimilation efficiency (Parton et al., 1993). HR minus NPP is the net ecosystem exchange (NEE), that is, the net carbon flux between ecosystem and atmosphere.

2.3. Stable carbon isotope

During the growing season (from May to October 2012), foliage samples of *Abies fabri* were collected between 2,800 m and 3,700 m at 100-m intervals along the altitudinal gradient of Mt. Gongga. At each altitude, we set out 50×100-m sampling quadrats, where four to five trees were selected for sampling. A total of 20-30 trees were selected at each altitude. Foliage samples were dried in a forced-draft oven at 65 °C for 48 h and then ground into a fine powder and stored at 4 °C until analysis.
The carbon isotopes were measured using an elemental analyzer (Flash EA1112 HT) interfaced to an isotope ratio mass spectrometer (MAT253, Thermo Fisher Scientific, Inc., USA) at the Chinese Academy of Forestry. Subsamples of the foliage biomass were analyzed for $^{13}\text{C}/^{12}\text{C}$ carbon isotope composition (expressed using delta-notation, $\delta^{13}\text{C}_{\text{VPDB},\%o}$) of CO$_2$ gas that was generated from the combustion of the dried foliage tissue in an elemental analyzer. The precision of the $\delta^{13}\text{C}$ measurements was 0.1% based on the standard deviation of repeated analyses. The ratio of stable carbon isotope (perl mil, ‰) is expressed as follows (Farquhar et al., 1989):

$$\delta^{13}\text{C}_p = \frac{R_{\text{sample}}}{R_{\text{std}}} - 1 \times 1000$$  \hspace{1cm} (11)

Where $R_{\text{sample}}$ and $R_{\text{std}}$ are the ratio of the heavy to light isotope in the sample and the international Vienna Pee Dee Belemnite carbon standard material, respectively.

Farquhar et al. (1982) showed that there was a relationship between the stable carbon isotope composition of leaf tissue and $c/_c_a$.

$$\delta^{13}\text{C}_p = \delta^{13}\text{C}_a - a - (b - a) \frac{c_i}{c_a}$$  \hspace{1cm} (12)

where $a$ is the isotopic fractionation during photosynthetic gas exchange caused by the slower diffusion of $^{13}\text{CO}_2$ in air (4‰), $b$ is the net fractionation associated with RuBP carboxylase activity (27‰), and $c_i$ and $c_a$ are the atmospheric and intercellular CO$_2$ concentrations, respectively.

WUE of the ecosystem from $\delta^{13}\text{C}_p$ measurements can be expressed by the following equation:

$$\text{WUE} = \frac{A}{E} \approx \frac{c_a-c_i(\delta^{13}\text{C}_p-\delta^{13}\text{C}_a-a)/(b-a)}{1.6\Delta W}$$  \hspace{1cm} (13)

where $\Delta W$ is the difference in the water vapor concentration between the intercellular
and ambient air, and the value 1.6 is the ratio of the stomatal conductance of water vapor to that of CO₂. In this study, \( \Delta W \) represents the saturated vapor pressure deficit.

### 2.4 Eddy covariance measurements

Eddy covariance measurements of the carbon flux, latent and sensible heats were collected in 2009 at 30-minute intervals. An open-path eddy covariance system was installed 30 m above the ground in an *Abies fabri* experimental plot at an altitude of 3000 m. The system consisted of an open-path infrared gas analyzer (Li-7500; Licor Inc., Lincoln, NB, USA) and a three-dimensional sonic anemometer (CSAT3; Campbell Scientific Inc., Logan, UT, USA). A data logger (CR3000; Campbell Scientific Inc., Logan, UT, USA) recorded the eddy covariance signals at 10 Hz for archiving and online computation.

A three-angle coordinate rotation approach was used to align the coordinates (Wilczak et al., 2001). The WPL method was used to adjust density changes resulting from fluctuations in heat and water vapor (Webb et al., 1980). The friction velocity threshold was empirically set as 0.2 m s\(^{-1}\) to filter nighttime fluxes. Spurious data were removed from the dataset if the instrument performance was abnormal or rainfall events occurred. The missing data accounted for approximately 35% of the total data. To compare the simulated carbon and water fluxes, the missing or rejected data were not interpolated. The energy balance closure was evaluated using linear regression coefficients between the 30-minute estimates of dependent flux variables (LE+H) against the independently derived available energy (Rn-G-S) (Wilson et al., 2002). The closure of the energy balance was acceptable, the slope of LE+H vs. Rn-G-S was 0.71
2.4. Definition of WUE

The amount of carbon gained per unit of water loss is named WUE. WUE has different definitions depending on the temporal and spatial scales of the processes (Steduto and Albrizio, 2005), while the different definitions of WUE refer to different ecological processes and therefore, different influencing factors. In this study, WUE was calculated using the following equations:

\[ WUE = \frac{GPP}{ET} \] (14)

\[ WUE = \frac{NPP}{ET} \] (15)

WUE calculated using Eq. 14 and Eq. 15 are controlled by both the physiological process of transpiration and the physical process of evaporation from the soil surface and the canopy.

\[ WUE = \frac{GPP}{Et} \] (16)

\[ WUE = \frac{NPP}{Et} \] (17)

WUE calculated using Eq. 16 and Eq. 17 reflect the water use ability of the plant community.

WUE calculated using Eq. 14 and Eq. 15 are on the ecosystem scale, while those calculated using Eq. 16 and Eq. 17 are on the plant scale. The difference is the sum of the canopy interception and soil evaporation.

2.5. Data and the validation of the model

The hourly meteorological data (January to December, 2012) used as model inputs, include the hourly mean air temperature, precipitation, relative humidity, wind velocity
and radiation, and were collected at altitudes of 2200 m, 3000 m, 3500 m and 4200 m by an auto meteorological observation system (AMOS) on Mt. Gongga. According to the observations of the four AMOSs, the wind velocity, relative humidity and total radiation rarely varied. Because our study was carried out in the Hailuogou valley on the same aspect, linear interpolation was used to interpolate the air temperature and precipitation along the elevation gradient every 100 m. Linear interpolation was used to derive the temperature and precipitation along the altitudinal gradient.

The model validation tests the degree of agreement between the simulated and measured values. The AVIM2 has been validated by many vegetation types in China, such as forest, crops, steppe and desert grassland (Lu and Ji, 2006; Huang et al., 2007; Ji et al., 2008). The modeled WUE, which is defined as GPP/Et, was validated by comparing the simulated value to that derived from δ13C. The results demonstrated that WUE (GPP/Et) simulated by the AVIM2 was generally in agreement in terms of temporal and altitudinal variations with the measured WUE (Fig. 1a, b). The analysis of R-squared (R²) and p value indicated that the simulated value had good accuracy. The simulated NEE was also compared with that observed by eddy covariance, and the results showed that the AVIM2 can capture the variance of NEE (Fig. 2).

The simulated ET was also validated with the value observed by eddy covariance. The AVIM2 can simulate the daily variation of the ET in the vegetative season or in the dormant season (Fig. 3). The components of the ET were also validated with the observed results. The Ein, T and Es were observed from April to October in 2009 (Lin et al., 2011; Sun et al., 2013). The simulated canopy interception was 402.8 mm,
compared to 460.7 mm in observations (Sun et al., 2013). The simulated transpiration
was 139.2 mm, which is almost the same as the observed value of 139.8 mm (Lin et al.,
2011). The simulated evaporation from the ground was 56.3 mm, which is higher than
the observed value of 44.2 mm (Lin et al., 2011). In conclusion, the AVIM2 was a
convincing method for the simulation of the carbon gain and water loss on Gongga
Mountain. Moreover, based on WUE derived from the $\delta^{13}$C, the ET, GPP and NPP
simulated using the AVIM2 are also reliable.

2.6. Data analysis

A one-way ANOVA with Fisher’s LSD test was performed to test the difference in
the GPP, NPP, ET and WUE of different months. The relationships between the ET, Et,
GPP and climatic variables were fitted with linear or non-linear equations using
SigmaPlot 12.3. All analyses were conducted with SPSS 13.0. Statistically significant
differences were set with $p < 0.05$.

3. Results

3.1. Seasonal variations of meteorological conditions

To reveal the relationship between WUE and climatic factors, the variation
patterns of the monthly precipitation, air temperature, vapor pressure deficit (VPD) and
net radiation ($R_n$) were investigated. The annual precipitation was 1896, 1606, 2022
and 1469 mm from 2008 to 2011 at an altitude of 3000 m (Fig. 4a). The annual mean
air temperature was 4.7, 5.3, 5.4 and 4.6 °C, and the highest monthly mean air
temperature occurred in July, while the coldest monthly mean air temperature was in
December, January or February (Fig. 4b). Compared with the air temperature, the VPD
had a similar trend (Fig. 4c). In contrast to the air temperature, the maximum value of the monthly net radiation was not in July, possibly due to the large amount of rainfall and cloudy weather that contributed to the variation in this seasonal trend (Fig. 4d). Therefore, the carbon gain and the water loss were promoted or inhibited by these environmental conditions.

3.2. Seasonal and altitudinal variations of GPP and NPP

The monthly variations in GPP and NPP at an altitude of 3000 m from 2008 to 2011 were simulated using the AVIM2. Over the 4 years, both the GPP and NPP showed obvious seasonal variations. The peak values of GPP and NPP occurred in July, while the smallest values occurred in January or February (Fig. 5). The annual GPP and NPP were 5.8, 5.8, 6.0 and 6.2 gCm$^{-2}$d$^{-1}$ from 2008 to 2011. The mean monthly variations of GPP and NPP for *Abies fabri* at an elevation of 3000 m were also modeled using the AVIM2. During the period of dormancy (from November to April of the next year), the GPP and NPP were lower compared with the vegetative season, but plant photosynthesis and respiration continued even in the coldest month (air temperature < -5 °C). The annual GPP and NPP were 21143.7 and 12355.3 kgC ha$^{-1}$ a$^{-1}$, respectively, at an altitude of 3000 m.

Both the GPP and NPP decreased as the altitude increased. The decreases were -0.09 and -0.03 g m$^{-2}$ s$^{-1}$/100 m for the GPP and NPP, respectively. Both the GPP and NPP showed peak values at 3000 m (Fig. 6). The temperature decreased as the altitude increased, while the precipitation increased from an altitude of 2800 m to an altitude of 3500 m, before decreasing as the altitude increased further.
3.3. Seasonal and altitudinal variations of ET and its components

ET consists of canopy interception, transpiration and evaporation from the ground.

The mean annual amounts of Eint, Et and Es at an altitude of 3000 m were 367.1, 247.7 and 91.5 mm, respectively. The ratio of annual Eint to ET was 51.3%. The ratio of Et increased from only 18.7% in January to a maximum of 43.5% in June. In contrast to the GPP and NPP, neither the Et nor the ET peaked in July (Fig. 7). The annual ET was 628, 640, 587 and 706 mm from 2008 to 2011. The annual Et was 187, 200, 195 and 248 mm from 2008 to 2011.

The ET decreased as the altitude increased (Fig. 8). The annual amount of Et decreased sharply. The ratio of Et to ET decreased from 48.9% at an altitude of 2800 m to 26.3% at an altitude of 3700 m. However, Eint had the inverse trend. More water was lost through Eint in the altitude range from 2800 m to 3700 m.

3.4. Seasonal and altitudinal variations of WUE

WUEs with different definitions all had a similar seasonal variation pattern: they were larger during the vegetative season and smaller after the vegetative season (Fig. 9). This pattern suggests that GPP/Et, GPP/Etotal, NPP/Et and NPP/Etotal were affected by meteorological conditions in different ways. However, the maximum values of GPP/Et and NPP/Et occurred in different months, which indicated that WUEs with different definitions were different from each other.

GPP/Et and NPP/Et increased significantly as the altitude increased (Fig. 10a), whereas the GPP/ET and NPP/ET increased from an altitude of 2800 to 3500 m and then slightly decreased from an altitude of 3600 to 3700 m (Fig. 10b). There exists a
yielding point at an altitude of 3000 m, and the GPP/ET and NPP/ET increased rapidly
under the altitude of 3000 m.

4. Discussion

4.1 The definition of water use efficiency

The different definitions of WUE in this study address the different characteristics
of the effects of ecosystem respiration and evaporation (canopy interception and
evaporation from ground) on the temporal and spatial patterns of ecosystem WUE.
Meanwhile, the WUE definitions were different for different levels of study. WUE is
usually defined as net or gross CO$_2$ assimilation at the cost of water loss via
transpiration at the canopy level. However, WUE is often defined as plant CO$_2$
assimilation at the cost of total water loss by ET at stand level. This discrepancy makes
it very difficult to compare WUEs of the same species derived from different water loss
and carbon gain components. The difference between GPP/Et and NPP/Et or between
GPP/ET and NPP/ET resulted from ecosystem respiration, which is sensitive to
temperature and soil moisture, whereas the difference between GPP/Et and GPP/ET or
between NPP/Et and NPP/ET is mainly determined by the ratio of Et/ET. The
transpiration and evaporation from the canopy and the soil were mainly controlled by
biological and environmental factors.

Forest ecosystems usually have high WUEs compared with grassland and cropland
ecosystems. Ponton et al. (2006) found that the value of GPP/ET were $1.7\pm0.5$, $3.6\pm$
$1.5$ and $5.4\pm1.6$ mgC/gH$_2$O in grasslands, aspen and Douglasfir forests, respectively.
WUE expressed by GPP/ET was $2.5$~$3.1$ mgC/gH$_2$O for $Abies fabri$ along the
altitudinal gradient from 2800 m to 3700 m on Mt. Gongga. Compared with the results reported in the literature, the values of GPP/ET in this research were in the normal range (Law et al., 2002; Ponton et al., 2006; Yu GR et al., 2008; Beer et al., 2009).

The annual values of GPP/T, GPP/ET, NPP/T and NPP/ET were 7.1, 2.9, 4.2 and 1.8 mgC/gH2O for *Abies fabri* at 3000 m on Mt. Gongga. Not only were the spatial and temporal variations in WUE with different definitions different, but there was a large amount of variation in the WUE value depending on the different definitions. Ito and Inatomi (2012) also found that the values of GPP/T and NPP/ET were 8.0 and 0.92 mgC/gH2O on the global scale. Meanwhile, GPP/T and NPP/ET were only weakly correlated on the spatial scale (Ito and Inatomi, 2012).

### 4.2 Seasonal patterns of water use efficiency

There was a significant correlation between the carbon gain and water loss (Fig. 13), while the $R^2$ between the GPP, NPP and Et was larger than that of the GPP, NPP and ET. Canopy interception was responsible for 51.3% of the total ET at 3000 m, and the contribution was even higher as the altitude increased. Therefore, this non-stomatal evaporation process reduced the strength of the correlation between the carbon gain and water loss through the stomata. The carbon gain increased sharply as the water loss increased when the monthly Et was less than 10 mm or the ET was less than 20 mm. The patterns of the variations in carbon gain and water loss were relatively constant throughout the vegetative season. The variations in WUE among different seasons, as reported in the literature (Yu GR et al., 2007), indicated that the coupled relationship between the carbon gain and water loss was influenced by changing climatic conditions.
The response of the carbon gain and water loss to climatic variables was different in various forest ecosystems (Keenan et al., 2013; Medlyn and De Kauwe, 2013). Understanding the effects of climatic variables on forest ecosystem productivity, WUE is useful for the prediction of changes in the carbon gain and water loss due to climate change (Law et al., 2002). In this study, the responsive characteristics of GPP, Et and ET to monthly precipitation, temperature, VPD and net radiation (Rn) were analyzed at an altitude of 3000 m.

The ET, Et and GPP responded to climatic variables differently. The relationships between ET, Et, GPP and monthly precipitation and VPD were fitted with quadratic functions (Fig. 14a, c). However, there were different relationships between ET, Et, GPP, temperature and Rn (Fig. 14b, d). Temperature vs GPP, Rn vs ET and Rn vs T were all fitted with linear functions. ET and Et decreased when P > 180 mm, while GPP decreased when the monthly average Rn > 1700 MJ m⁻² d⁻¹. The asynchronous responses of ET, Et and GPP to changing climatic variables determined the relationship between the carbon gain and water loss. Therefore, WUE with different definitions varied during the month. The increasing rate of the ET and Et were much larger than those of the GPP and NPP in the vegetative season. Although ET, Et and GPP were fitted using the same mathematical form for monthly precipitation and VPD, the extent to which these variations were due to climatic factors was different.

4.3 Elevation gradients of water use efficiency

An elevation gradient is not a phenomenological driving variable. However, it is the combination of multiple factors, such as precipitation, temperature, nutrients and
plant physiology. The variation in precipitation had no significant influence on WUE of *Abies fabri* along an altitudinal gradient in the Gongga Mountains (Fig. 11a), which agreed with previous results (Li CY et al., 2009, Luo et al., 2011). A study in the Hawaiian Metrosideros found that the δ13C value of bulk leaf tissue increased as the altitude increased in the eastern humid region, while the same trend did not exist in the western arid region (Vitousek et al., 1990). The annual rainfall was more than 1600 mm between 2800 m and 3700 m on the subalpine Gongga Mountain. Van de Water et al. (2002) found that water was not the main influencing factor in the wet area. Therefore, we concluded that the variation in the WUE along the altitudinal gradient was mainly determined by other factors.

There was a significant negative relationship between the air temperature and WUE derived from the δ13C of bulk leaf tissue (Fig. 11b), which also indicated that the intrinsic WUE increased as the air temperature decreased along the altitudinal gradient. The curves of GPP and Et against temperature were different (Fig. 11b). Temperature is an important climatic variable in mountainous terrain. The thicknesses and hardesses of leaves change to adapt to low temperature environments, while the diffusion resistance to CO2 also increases (Taylor and Sexton., 1972). As the diffusivity decreased under low air temperature and soil temperature conditions, the stomatal conductance also decreased (Panek and Warning, 1995). The transpiration was restricted because the water potential of leaves increased when the air temperature and soil temperature were low (Cochard et al., 2000). Therefore, the δ13C of bulk leaf tissue increased. Meanwhile, the GPP/Et and NPP/Et increased along the altitudinal gradient.
The δ¹³C of bulk leaf tissue increased as the leaf nitrogen content increased (R²=0.9368, p<0.01) and decreased as the specific leaf area increased (R²=0.9426, p<0.01) (Fig. 12a, b). Hultien et al. (2000) found that a negative relationship existed between the δ¹³C of bulk leaf tissue of a coniferous forest and the specific leaf area along an altitudinal gradient in the northern Rocky Mountains. Li MH et al. (2008) also demonstrated that the specific leaf area of a dark coniferous forest decreased as the altitude increased. However, there was a positive relationship between the δ¹³C of bulk leaf tissue and the specific leaf area for Quercus aquifolioides in a subalpine area of western Sichuan Province (Li CY et al., 2009). There was also a negative relationship between the δ¹³C of bulk leaf tissue and the specific leaf area during the seasonal variation of Abies fabri at 3000 m on Gongga Mountain (Luo TX et al., 2011). Nitrogen is the main component of the photosynthetic enzyme and is also one of the main factors that determine the photosynthetic capacity of a leaf. An increase in the leaf nitrogen content can augment the content of leaf chlorophyll and carboxylase and therefore influence the stomatal density and leaf thickness. Many studies have shown that the leaf nitrogen content of alpine plants increases as the altitude increases (Friend et al., 1989; Körner, 1989; Li CY et al., 2009). In the subalpine mountains, more nitrogen is distributed to the leaf, thereby offsetting the decrease in photosynthetic rate caused by low light and low nitrogen use efficiency.

Farquhar et al. (1982, 1989) showed that the stable carbon isotope composition of leaf tissue was related to ci/ca. The stomatal conductance was influenced by climatic variables and physiological function. In our study, both the value of ci/ca and ci...
decreased as the altitude increased. Therefore, both the transpiration and carbon gain decreased along the altitudinal gradient (Fig. 6, 8). However, the way in which the variation in the transpiration to carbon gain ratio responded to stomatal resistance under changing environmental conditions was different. Keenan et al. (2013) also found that the effects of stomatal control on the carbon gain and water loss were different. The carbon gain is more sensitive to variations in conductance than the water loss (Li SE et al., 2015). Therefore, GPP/T and NPP/T showed significant increases from low altitudes to high altitudes, while the canopy interception increased along the elevation gradient due to changes in the amount of rainfall. GPP/ET and NPP/ET only showed moderately increasing trends along the elevation gradient.

5 Conclusion

Based on experimental data and modeled data, we analyzed the temporal and altitudinal variations of the carbon gain, water loss and WUE and discussed the mechanisms of climatic variables, specific leaf area and leaf nitrogen content that control the carbon gain, water loss and WUE in a subalpine coniferous forest. WUE was defined using different carbon gain and water loss components. On the monthly scale, the carbon gain and water loss had different relationships with the precipitation, air temperature, VPD and net radiation, indicating that a variety of climatic variables drove the photosynthesis and ET in different ways and at different rates. On the altitudinal scale, the carbon gain, ET and T decreased as the altitude increased, while the GPP/T and NPP/T increased significantly as the altitude increased. However, the GPP/ET and NPP/ET increased from 2800 to 3500 m and then decreased. Canopy
interception played an important role in the variation of WUE with different definitions along the elevation gradient. WUE had a positive relationship with the specific leaf area and a negative relationship with temperature and leaf nitrogen content along the altitudinal gradient.

The response of the carbon gain and water loss to environmental and physiological changes on the temporal and altitudinal scales is complex, which is also a great challenge for water resource management and forest management. How the carbon gain, water loss and WUE for the subalpine mountainous forest ecosystem varies with changes in the global climate still remains to be investigated. Improved understanding on temporal and altitudinal behavior of carbon and water vapour exchanges in relation to environmental conditions will enhance our ability to predict the effects of changing climate on mountainous ecosystems.

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Fig. 1 Modeled and measured annual water use efficiency (WUE=GPP/Et) of *Abies fabri* along an altitudinal gradient from 2800 m to 3700 m in 2011 (the dashed line is 1:1 line) (a), and temporal pattern from May to October on elevation of 3000 m in 2011 (b).
Fig. 2 Simulated NEE and the NEE deduced from eddy-covariance based measurements over half an hour from the 164th to the 173rd day of 2009 at an altitude of 3000 m (DOY is the day of year).
Fig. 3 Simulated ecosystem evapotranspiration (ET) and the ET deduced by eddy-covariance based measurements over half an hour from the 59th to the 61st (a) and the 168th to the 170th (b) days of 2009 at an altitude of 3000 m (DOY is the day of year).
Fig. 4 The seasonal variation of precipitation (a), air temperature (b), VPD (c) and net radiation (d) from 2008 to 2011 at an altitude of 3000 m.
Fig. 5 The seasonal variation of monthly gross primary productivity (GPP), net primary productivity (NPP), evapotranspiration (ET) and transpiration (Et) simulated by the AVIM2 from 2008-2011.
Fig. 6 Precipitation, temperature, GPP and NPP change along an altitudinal gradient from 2800 to 3700 m on Mt. Gongga (the solid line with solid circles is GPP, the dashed line with hollow circles is NPP, the red line is air temperature, and the gray bar is precipitation).
Fig. 7 Seasonal variation in the components of evapotranspiration (mean ± SE) at an altitude of 3000 m in 2012 (Eint is canopy interception, Es is soil evaporation, Et is transpiration). Eint, Es and Et were simulated by the AVIM2.
Fig. 8 Variation in evapotranspiration (ET) and its components (canopy interception, Eint; soil evaporation, Es; transpiration, Et) along an altitudinal gradient between 2800 and 3700 m.
Fig. 9 The simulated seasonal variation of GPP/Et (mean ± SE), GPP/Etotal (mean ± SE), NPP/Et (mean ± SE) and NPP/Etotal (mean ± SE) on Mt. Gongga.
Fig. 10 The simulated spatial variation of GPP/Et, GPP/ET, NPP/Et and NPP/ET along an altitudinal gradient from 2800 to 3700 m on Mt. Gongga.
Fig. 11 The relationship between water use efficiency (derived from δ13C of bulk leaf tissue) (black solid circles with standard error), GPP (black open circles), Et (black open triangles) and precipitation (a) or temperature (b) along an altitudinal gradient from 2800 m to 3700 m.
Fig. 12 The relationship between the $\delta^{13}$C of bulk leaf tissue and the specific leaf area or the leaf nitrogen content along an altitudinal gradient from 2800 m to 3700 m.
Fig. 13 The relationship between monthly gross primary productivity (GPP), net primary productivity (NPP), transpiration (Et) and evapotranspiration (ET) at an altitude of 3000 m from 2008 to 2011 (y = a*lnx + b).
Fig. 14 The relationship between monthly evapotranspiration (ET), transpiration (Et), gross primary productivity (GPP), and climatic variables (precipitation, temperature, saturated vapor pressure deficit (VPD) and net radiation (Rn)) at an altitude of 3000 m from 2008 to 2011.
<table>
<thead>
<tr>
<th>Altitude Range</th>
<th>Precipitation Variation</th>
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<tbody>
<tr>
<td>2800-3000</td>
<td>+5%/100 m</td>
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<tr>
<td>3000-3500</td>
<td>+5%/100 m</td>
</tr>
<tr>
<td>3500-3700</td>
<td>-5.7%/100 m</td>
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Table 1: Variation in precipitation every 100 m along an altitudinal gradient using four meteorological stations at each site.