J. Geogr. Sci. 2011, 21(4): 651-665
DOI: 10.1007/s11442-011-0870-5

Patterns and driving factors of WUE and NUE in natural forest ecosystems along the North-South Transect of Eastern China

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Abstract: From July 2008 to August 2008, 72 leaf samples from 22 species and 81 soil samples in the nine natural forest ecosystems were collected, from north to south along the North-South Transect of Eastern China (NSTEC). Based on these samples, we studied the geographical distribution patterns of vegetable water use efficiency (WUE) and nitrogen use efficiency (NUE), and analyzed their relationship with environmental factors. The vegetable WUE and NUE were calculated through the measurement of foliar $\delta^{13}C$ and C/N of predominant species, respectively. The results showed: (1) vegetable WUE, ranging from 2.13 to 28.67 mg C g^{-1} H_2O, increased linearly from south to north in the representative forest ecosystems along the NSTEC, while vegetable NUE showed an opposite trend, increasing from north to south, ranging from 12.92 to 29.60 g C g^{-1} N. (2) Vegetable WUE and NUE were dominantly driven by climate and significantly affected by soil nutrient factors. Based on multiple stepwise regression analysis, mean annual temperature, soil phosphorus concentration, and soil nitrogen concentration were responding for 75.5% of the variations of WUE ($p<0.001$). While, mean annual precipitation and soil phosphorus concentration could explain 65.7% of the change in vegetable NUE ($p<0.001$). Moreover, vegetable WUE and NUE would also be seriously influenced by atmospheric nitrogen deposition in nitrogen saturated ecosystems. (3) There was a significant trade-off relationship between vegetable WUE and NUE in the typical forest ecosystems along the NSTEC ($p<0.001$), indicating a balanced strategy for vegetation in resource utilization in natural forest ecosystems along the NSTEC. This study suggests that global change would impact the resource use efficiency of forest ecosystems. However, vegetation could adapt to those changes by increasing the use efficiency of shortage re-

Received: 2010-10-26 **Accepted:** 2010-02-20
Foundation: National Natural Science Foundation of China, No.30590381; No.31000211; National Basic Research Program of China, No.2010CB833504
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source while decreasing the relatively ample one. But extreme impacts, such as heavy nitrogen deposition, would break this trade-off mechanism and give a dramatic disturbance to the ecosystem biogeochemical cycle.

Keywords: water use efficiency (WUE); nitrogen use efficiency (NUE); δ^{13}C; C/N; North-South Transect of Eastern China (NSTEC)

1 Introduction

What would happen to the structure and the function of terrestrial ecosystems, as a result of elevated atmospheric CO_2 (IPCC, 2007), increased temperature (Dore, 2005), changed precipitation pattern (Zhai *et al*., 2004), or rising atmospheric nitrogen deposition (Galloway *et al*., 2004), has been a hot issue under the background of global change. Carbon cycle is a key point in study on the impacts of global change on terrestrial ecosystem biogeochemical cycle and its adaption. Water and nutrient supply in terrestrial ecosystems restricts carbon cycle (Felzer *et al*., 2009), and brings uncertainty for the effect of terrestrial ecosystems on climate change mitigating (Beedlow and Tingey *et al*., 2004). Efficient use of water and nitrogen was critical for plant growth, survival and health (Xiao *et al*., 2004).Water use efficiency (WUE) and nitrogen use efficiency (NUE) provide useful indexes for a better understanding of the relationship between environmental resources and the cycle coupling of carbon, water, and nitrogen properties (Luo *et al*., 2004; Hu *et al*., 2009).

Terrestrial transect is a suitable platform for studies to understand how terrestrial ecosystems would respond to global change by the substitution method of space for time (Wu *et al*., 2010, Zhou *et al*., 2002). Examining the spatiotemporal variations in WUE and NUE across a large transect is useful for predicting the effects of global change on carbon, water, and nitrogen cycling, and evaluating the disturbance to their balances in terrestrial ecosystems. Further, the results of such examination benefit shaping and implementing effective land-management strategies (Thuiller *et al*., 2003). Much control experiment research has sought to improve our knowledge of the water and nitrogen condition impact on WUE and NUE (Sun *et al*., 2006, Li *et al*., 2003), but very few reports have documented the spatial variations in WUE and NUE in China's forest ecosystems. Because of the mechanisms that improve plant growth and chances of survival under resource limitation may incur costs which reduce growth or survivability in unstressful conditions, the variations of WUE and NUE might not have the same results along a large transect as that in control experiments.

The North-South Transect of Eastern China (NSTEC) is a forest concentrated distribution area in China (He *et al*., 2008), and spans a wide range of environmental conditions, including temperature, precipitation, and nitrogen deposition. Therefore, the NSTEC is an ideal place to study the carbon, nitrogen and water cycles in forest ecosystems in East Asian monsoon region. In this study, we chose the typical forest ecosystems along the NSTEC. Through measuring the foliar δ^{13}C and C/N of predominant species, we described the pattern of vegetable WUE and NUE and analyzed the relationships between vegetable WUE or NUE and environmental factors. The objectives of this study were: (1) to determine the patterns of vegetable WUE and NUE in typical forest ecosystems along the NSTEC; (2) to uncover the driving factors of the variation of vegetable WUE and NUE; (3) to find out whether there would be a trade-off between vegetable WUE and NUE or not in the natural forest ecosystems along the transect with significant environmental gradients.

2 Materials and methods

2.1 Study areas

The NSTEC is from Hainan Island to the northern border of China, ranging from longitude 108˚–118˚E for latitude less than 40˚N and from longitude 118–128°E for latitude equal to or greater than 40°N, embraces 25 provinces, and covers about 1/3 of the territory of China (Figure 1). Because of the influence of the East Asian monsoon, the climate in Asia differs from that in Europe and North America, with apparent latitudinal gradients of temperature and precipitation along the NSTEC (Yu *et al*., 2008). Zonal forest ecosystems are distributed along the NSTEC (Yu *et al*., 2006), including cold-temperate coniferous forest, temperate mixed forest, warm-temperate deciduous broad-leaved forest, subtropical evergreen broad-leaved forest, and tropical monsoon rainforest from north to south. Along the NSTEC, we chose nine research sites to investigate vegetable WUE and NUE of natural forest ecosystems. Sampling site characteristics were described in Table 1.

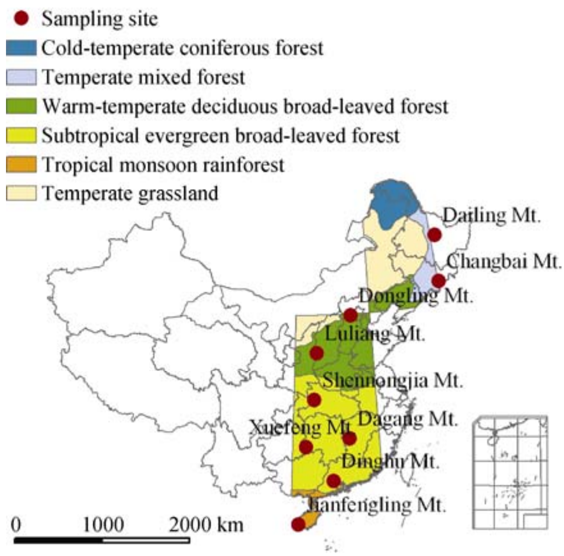

Figure 1 Vegetation regionalization and sampling sites along the NSTEC
The NSTEC was colored with different color representing different types of vegetation

2.2 Sample collection

From July to August 2008, leaf and soil samples were collected in the representative forest ecosystems from north to south along the NSTEC. In order to eliminate the system deviation, only broad-leaved predominant species were selected as samples to characterize the representative forest ecosystems. Three mature individual trees of each predominant species with middle breast height diameter were randomly selected in the forest stand for collecting leaf samples. Each tree was open-grown, with full southern sun exposure. Fully mature leaves were sampled from the tips of south-facing branches in the lower crown by a tall trees

Table 1 Description of the sampling site characteristics

Sampling sites	Location	Elevation (m)	MAT [a] (℃)	MAP [b] (mm)	ANDF [c] (N hm^{-2} a^{-1})	Soil type
Dailing Mt.	45.4°N, 127.5°E	703	1.1	663.6	11.3	Dark brown forest soil
Changbai Mt.	42.4°N, 128.1°E	738	3.0	714.1	17.5	Dark brown forest soil
Dongling Mt.	42.0°N, 115.4°E	1100	6.6	508.9	23.3	Cinnamon soil
Luliang Mt.	36.3°N, 110.8°E	1320	10.0	575.9	16.1	Cinnamon soil
Shennongjia Mt.	31.5°N, 110.4°E	1027	11.6	1114.1	22.5	Brown soil
Dagang Mt.	27.5°N, 114.5°E	652	17.0	1633.7	7.9	Yellow soil
Xuefeng Mt.	26.7°N, 109.4°E	427	15.6	1393.6	18.3	Lateritic red soil, yellow soil
Dinghu Mt.	23.2°N, 112.5°E	300	22.2	1771.1	38.4	Lateritic red soil, yellow soil
Jianfengling Mt.	18.6°N, 108.7°E	542	22.9	1408.1	8.8	Latosol

Sampling sites	Forest type	Predominant broad-leaved species
Dailing Mt.	Conifer and broad-leaved mixed forest	*Betula costata*, *Tilia amurensis*
Changbai Mt.	Conifer and broad-leaved mixed forest	*Tilia amurensis*, *Acer mono, Quercus mongolica*, *Fraxinus mandshurica*
Dongling Mt.	Deciduous broad-leaved forest	*Quercus liaotungensis*, *Betula dahurica*
Luliang Mt.	Deciduous broad-leaved forest	*Quercus liaotungensis*, *Populus davidiana, Quercus variabilis*
Shennongjia Mt.	Evergreen broad-leaved forest	*Cyclobalanopsis multinervis*, *Ulmus bergmanniana schneid*, *Alstonia scholaris*
Dagang Mt.	Evergreen broad-leaved forest	*Schima argentea*, *Elaeocarpus sylvestris*
Xuefeng Mt.	Evergreen broad-leaved forest	*Machilus pauhoi*, *Castanopsis fragesii*
Dinghu Mt.	Monsoon evergreen broad-leaved forest	*Schima superba*, *Castanopsis chinensis*, *Acmera acuminatisima*
Jianfengling Mt.	Monsoon rainforest	*Vatica mangachapoi*, *Liquidambar formosana*, *Amesiodendron chinensis*

[a] MAT: Mean annual temperature and values are the averages from 1985 to 2008; [b] MAP: Mean annual precipitation and values are the averages from 1985 to 2008; [c] ANDF: Annual nitrogen deposition flux and values are the averages from 2000 to 2009. Data source: The database of Chinese Ecosystem Research Network (CERN)

trimmer. Leaves were collected from a couple of individuals of each plant and then combined into one samples.

Three sets (replicas) of soil profile samples (5–6 m apart) were collected from three depths (0–10, 10–20, and 20–30 cm). To reduce spatial heterogeneity, the soil at each depth for one set of samples was collected from three cores (holes, about 0.5–1.0 m apart) using a soil corer. Foliar samples were dried to constant weight at 65℃. Mineral soils were air dried at room temperature and then sieved through a 2 mm sieve to remove roots, gravel and stones. All samples were ground into fine powder with a planetary mill and saved in glassware. Plant and soil samples would be oven dried at 65℃ for 24 h before analysis. Finally, we obtained 72 leaf samples from 22 species and 81 soil samples in the nine natural forest ecosystems.

2.3 C, N concentrations and $\delta^{13}C$ measurement

Carbon, nitrogen concentrations and $\delta^{13}C$ values were determined simultaneously with an automatic, online elemental analyzer (Flash EA1112, ThermoFinnigan, Milan, Italy) coupled to an isotope ratio mass spectrometer (IRMS) (Finnigan MAT 253, Thermo Electron, Bremen, Germany). Standard deviation of 10 repeated samples was <0.4‰. Results of the IRMS measurement were given in δ notation. δ values of isotope of ^{13}C were expressed in per mil (‰), and calculated as follows (Craig, 1957):

$$\delta(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \tag{1}$$

where R_{sample} and R_{standard} are the carbon isotopic ratio ($^{13}C/^{12}C$) of sample and standard, respectively. The standard is Vienna-Pee Bee Belemnite (V-PDB). A positive (negative) $\delta^{13}C$ value indicates the enrichment (depletion) of the heavy isotope relative to the light one according to a known standard.

2.4 WUE and NUE calculation

The ^{13}C natural abundance of C_3 plants provides a useful measurement of integrated carbon/water balance in plants over a longer time interval, because of the well correlated relationship between foliar $\delta^{13}C$ and the ratio between intercellular CO_2 concentration (c_i) and free air CO_2 concentration (c_a) (Farquhar *et al.*, 1982),

$$\delta^{13}C = \delta^{13}C_a - a - (b - a)\frac{c_i}{c_a} \tag{2}$$

where $\delta^{13}C_a$ is the ^{13}C abundance of free air (–8‰), and a, b are the isotope fractionation during CO_2 diffusion and carboxylation, respectively. As for the C_3 plant, a and b are equal to 4.4‰ and 27‰, respectively.

WUE is the ratio between photosynthetic rate (A) and transpiration rate (E),

$$\text{WUE} = \frac{A}{E} = \frac{g_s(c_a - c_i)/1.6}{g_s(e_i - e_a)} = \frac{c_a(1 - c_i/c_a)}{1.6 \times (e_i - e_a)} = \frac{c_a(1 - c_i/c_a)}{1.6 \times \text{VPD}} \tag{3}$$

where g_s is the stomatal conductance, and e_i and e_a are inner and outer vapour pressure of diachyma, respectively. The difference between e_i and e_a is used to be substituted by vapour pressure deficit (VPD), because of the difficulty in measurement.

Based on Eq.2, Eq.3, and the measurement value of $\delta^{13}C$ and annual mean VPD, the long-term vegetable WUE of each plant was calculated.

NUE was defined as the ratio between photosynthetic rate and leaf nitrogen content (Berendse and Aerts, 1987),

$$\text{NUE} = \frac{A}{N_{\text{leaf}}} = \frac{dW}{dt} \times \frac{1}{N_{\text{leaf}}} \tag{4}$$

where W is the biomass, and plant long-term average NUE could be estimated by foliar C/N (Livingston *et al.*, 1999).

2.5 Statistical analysis

The sample differences of foliar $\delta^{13}C$, C and N concentrations, WUE, and NUE were tested with analysis of variance (ANOVA). Means comparison was done with Tukey's HSD test.

Regression analysis was used to test the relationship between WUE or NUE and environmental factors. All the analyses were conducted by SPSS software package. Statistically significant difference was set as $p<0.05$ unless stated otherwise.

3 Results

3.1 Foliar ^{13}C abundance and C, N concentrations

Figure 2 showed that foliar ^{13}C abundance of predominant species along the NSTEC ranged from –33.65 ‰ to –26.50 ‰, with an average value of –32.81‰. The average foliar ^{13}C abundance was the lowest in tropical monsoon rainforest ecosystem and the highest in warm-temperate deciduous broad-leaved forest ecosystem. While, there was no significant difference in foliar ^{13}C abundance of broad-leaved plant between temperate mixed forest ecosystem and subtropical evergreen broad-leaved forest ecosystem (Figure 2A).

Foliar N concentration of predominant species along the NSTEC ranged from 14.80 g kg^{-1} to 34.73 g kg^{-1}, with an average value of 23.56 g kg^{-1}. Foliar N concentration in tropical and subtropical forest ecosystems was significantly lower than that in temperate and warm-temperate forest ecosystems ($p<0.05$). Moreover, there was also significant difference between the two temperate forest ecosystems ($p<0.05$) (Figure 2B).

Foliar C concentration of predominant species along the NSTEC ranged from 405.96 g kg^{-1} to 505.63 g/kg, with an average value of 462.20 g kg^{-1}. The average foliar C concentration (428.04 g kg^{-1}) of predominant species in tropical forest ecosystem was significantly lower than that in other forest ecosystems ($p<0.05$). Evident difference also existed between subtropical forest ecosystem and warm temperature forest ecosystem ($p<0.05$) (Figure 2C).

3.2 WUE and NUE values

The value of vegetable WUE increased from 2.13 mg C g^{-1} H_2O in the tropical monsoon forest ecosystem to 28.67 mg C g^{-1} H_2O in the temperature mixed forest ecosystem, with the average value being 13.39 mg C g^{-1} H_2O. The magnitude followed the order: tropical monsoon rainforest < subtropical evergreen broad-leaved forest < warm-temperate deciduous broad-leaved forest < temperate mixed forest. Vegetable WUE in tropical monsoon forest ecosystem was significantly lower than that in other forest ecosystems ($p<0.05$), while vegetable WUE in temperate mixed forest ecosystem was significantly higher than that in other forest ecosystems ($p<0.05$). There was no obvious difference in vegetable WUE between subtropical forest ecosystem and warm temperature forest ecosystem (Figure 3A).

The average vegetable NUE value of predominant species in forest ecosystem along the NSTEC was 20.50 g C g^{-1} N. Vegetable NUE in tropical and subtropical forest ecosystems, ranged from 18.57 g C g^{-1} N to 29.60 g C g^{-1} N, was significantly higher than that in temperate and warm-temperature forest ecosystems ($p<0.05$), which ranged from 12.92 g C g^{-1} N to 21.90 g C g^{-1} N. There was no evident difference in vegetable NUE between tropical and subtropical forest ecosystem. However, the difference of vegetable NUE between the warm-temperature forest ecosystem and temperature forest ecosystem was obvious ($p<0.05$) (Figure 3B).

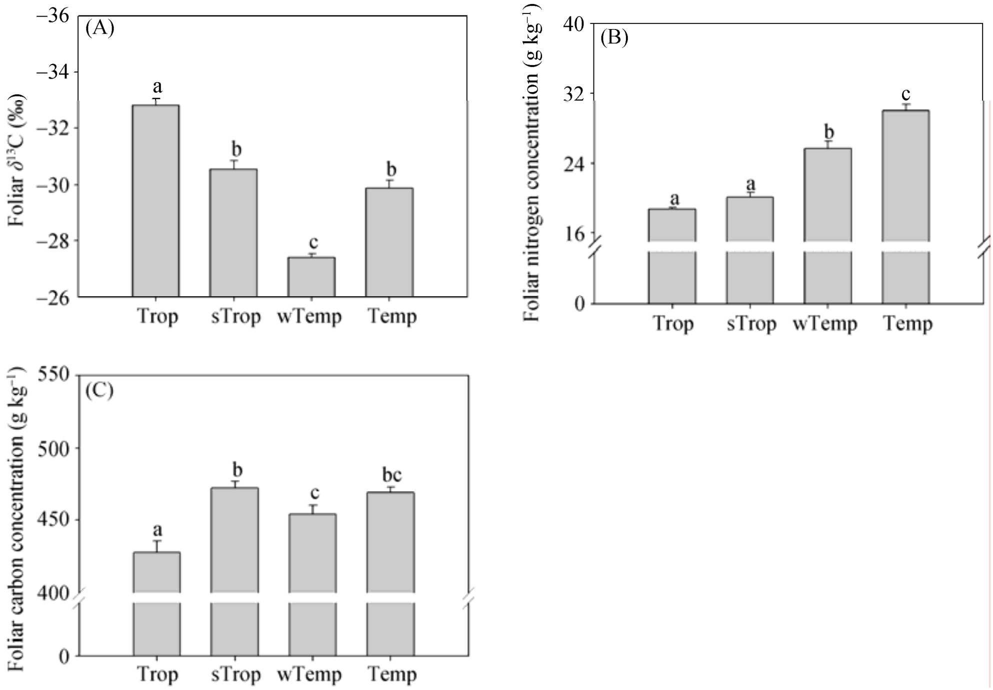

Figure 2 Variation of foliar δ^{13}C abundance (A), foliar nitrogen concentration (B), and foliar carbon concentration (C) of perdominant species in different forest ecosystems along the NSTEC

Trop: tropical monsoon rainforest; sTrop: subtropical evergreen broad-leaved forest; wTemp: warm-temperate deciduous broad-leaved forest; Temp: temperate coniferous and broad-leaved mixed forest. Error bars indicate standard errors (n = 3) of mean. Lowercase letters beside the means indicate statistical differences among the means for leaves at the level of $\alpha = 0.05$.

3.3 Latitudinal distribution of WUE and NUE

Vegetable WUE in forest ecosystems was increasing gradually from south to north along the NSTEC (Figure 4A). On the contrary, NUE of the predominant species in the forest ecosystems decreased as the latitude rising, although the varity of vegetable NUE was relatively unconspicuous in the southern end of the NSTEC (Figure 4B).

3.4 Relationship between resources use efficiency and climate factors

We compared the responsive characteristics of vegetable WUE and NUE to mean annual temperature (MAT) and mean annual precipitation (MAP) in typical forest ecosystems along the NSTEC (Figure 5). It is shown that the response of vegetable resources use efficiency to MAT or MAP was obviously different along the NSTEC. The vegetable WUE and MAT was negatively correlated ($p<0.001$) (Figure 5A), and MAT responded for over 60% of the variations of vegetable WUE. However, vegetable NUE was significantly and positively correlated with MAT ($p<0.001$) (Figure 5B). Vegetable WUE decreased linearly with increasing MAP, and the relation was significant at the level of $p<0.001$ (Figure 5C), while the relationship between vegetable NUE and MAP was significantly positive with logarithmic growth ($p<0.001$) (Figure 5D). MAP responded for 38.7% and 56.3% of the variations of vegetable WUE and NUE in typical forest ecosystems along the NSTEC, respectively.

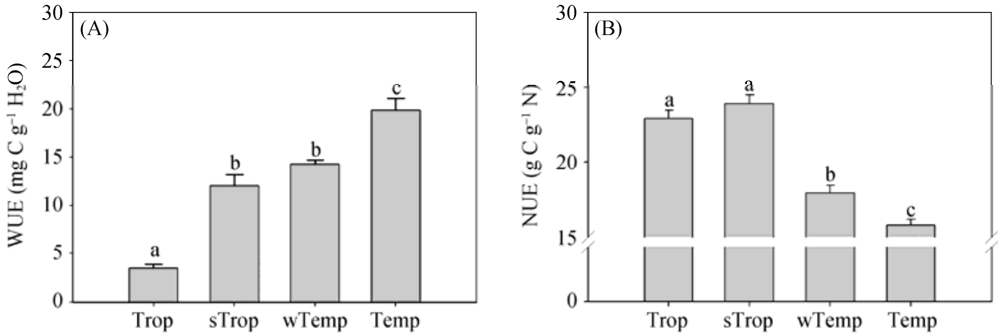

Figure 3 Variation of vegetable WUE and NUE in different forest ecosystems along the NSTEC
Trop: tropical monsoon rainforest; sTrop: subtropical evergreen broad-leaved forest; wTemp: warm-temperate deciduous broad-leaved forest; Temp: temperate coniferous and broad-leaved mixed forest. Error bars indicate standard errors (n = 3) of mean. Lowercase letters beside the means indicate statistical differences among the means for leaves at the level of α = 0.05.

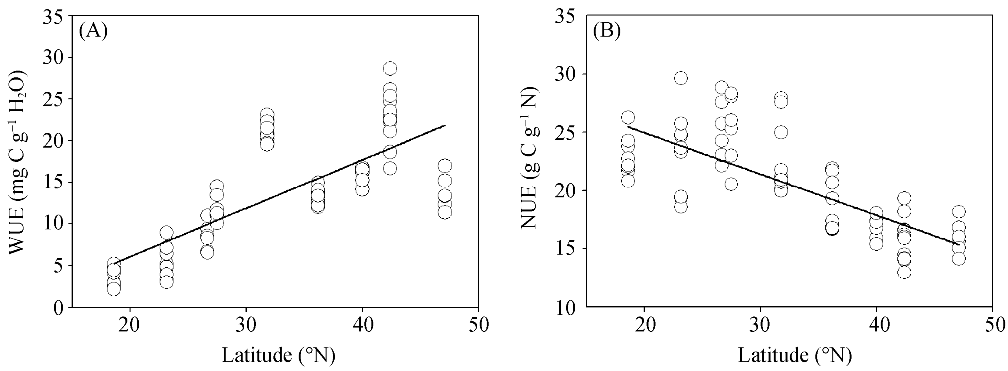

Figure 4 Latitudinal trends of vegetable WUE and NUE of dominant species in the typical forest ecosystems along the NSTEC

3.5 Relationship between resource use efficiency and nutrient factors

Soil nitrogen and phosphorus concentrations in different soil horizons under forest ecosystems were shown in Table 2. Soil nitrogen concentration and soil phosphorus concentration had consistently positive impacts on vegetable WUE in the typical forest ecosystems along the NSTEC (Figures 6A and 6C). The relationship between vegetable WUE and the soil nutrition conditions was significant (p<0.001). Soil nitrogen concentration and soil phosphorus concentration could explain 34.4% and 19.9% of the change in vegetable WUE, respectively. On the contrary, soil nitrogen concentration and soil phosphorus concentration had notably negative influences on vegetable NUE of predominant species in typical forest ecosystems along the NSTEC (p<0.001) (Figures 6B and 6D). Atmospheric nitrogen deposition flux exerted positive influence on vegetable WUE when the deposition level was below 25 kg N hm^{-2} a^{-1}, above which the ecosystem is considered as nitrogen saturated (Fang *et al*., 2008) (Figure 6E). Nitrogen deposition had negative impact on vegetable NUE, but the relationship between vegetable NUE and nitrogen deposition flux was not significant, even where the forest ecosystem was far from nitrogen saturated (Figure 6F).

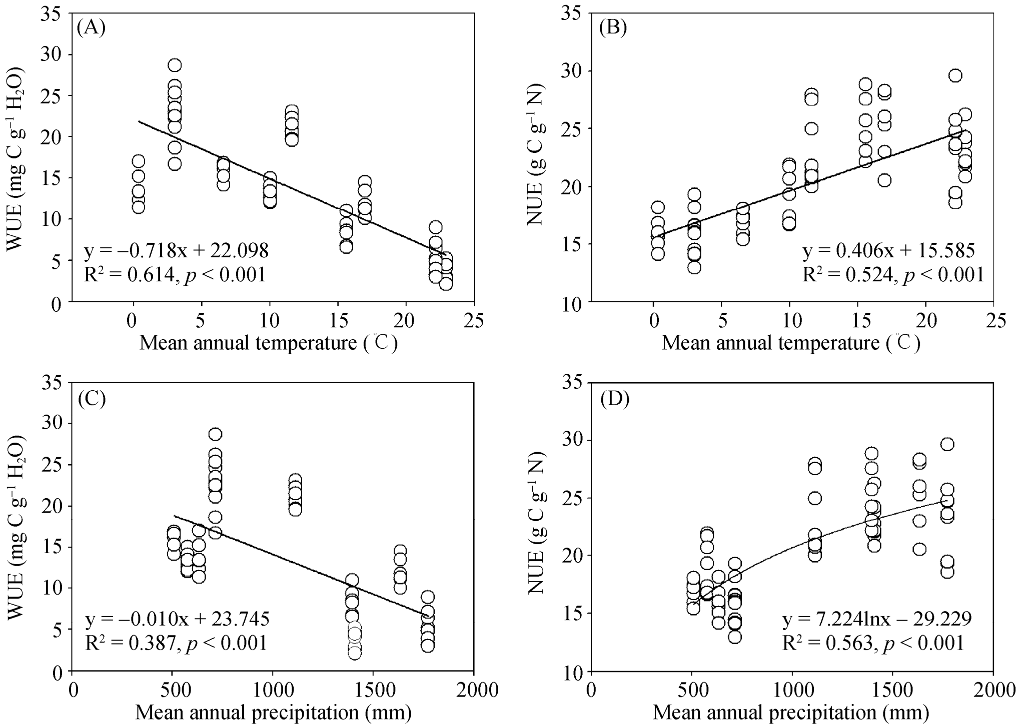

Figure 5 Relationship between vegetable WUE/NUE and climate factors

Table 2 Soil nitrogen and phosphorus concentrations in different soil horizons under forest ecosystems

Sampling sites	Soil nitrogen concentration (g kg^{-1})			Soil phosphorus concentration (g kg^{-1})		
	0–10 cm	10–20 cm	20–30 cm	0–10 cm	10–20 cm	20–30 cm
Dailing Mt.	7.11 (0.11)	4.40 (0.32)	2.71 (0.06)	1.33 (0.03)	1.14 (0.10)	1.01 (0.04)
Changbai Mt.	13.0 (0.44)	7.99 (0.34)	4.33 (0.02)	1.03 (0.13)	0.94 (0.14)	0.73 (0.03)
Dongling Mt.	3.21 (0.57)	1.70 (0.27)	0.87 (0.13)	0.36 (0.11)	0.29 (0.07)	0.35 (0.14)
Luliang Mt.	1.45 (0.27)	0.58 (0.07)	0.51 (0.12)	0.69 (0.06)	0.56 (0.03)	0.59 (0.04)
Shennongjia Mt.	2.43 (0.25)	1.68 (0.10)	1.14 (0.19)	0.26 (0.06)	0.35 (0.06)	0.35 (0.03)
Dagang Mt.	1.16 (0.38)	0.61 (0.03)	0.55 (0.04)	0.13 (0.07)	0.11 (0.07)	0.09 (0.07)
Xuefeng Mt.	1.70 (0.07)	1.36 (0.12)	1.13 (0.12)	0.12 (0.05)	0.14 (0.01)	0.13 (0.02)
Dinghu Mt.	3.25 (0.49)	2.04 (0.24)	1.46 (0.14)	0.44 (0.06)	0.38 (0.18)	0.31 (0.07)
Jianfengling Mt.	2.30 (0.30)	1.48 (0.07)	0.95 (0.10)	0.22 (0.15)	0.22 (0.08)	0.21 (0.09)

Mean (±1 SE), n=3

Based on multiple stepwise regression analysis, the results showed that vegetable WUE along the NSTEC was mainly controlled by mean annual temperature, soil phosphorus concentration, and soil nitrogen concentration. While, vegetable NUE was dominantly affected by mean annual precipitation and soil phosphorus concentration (Table 3).

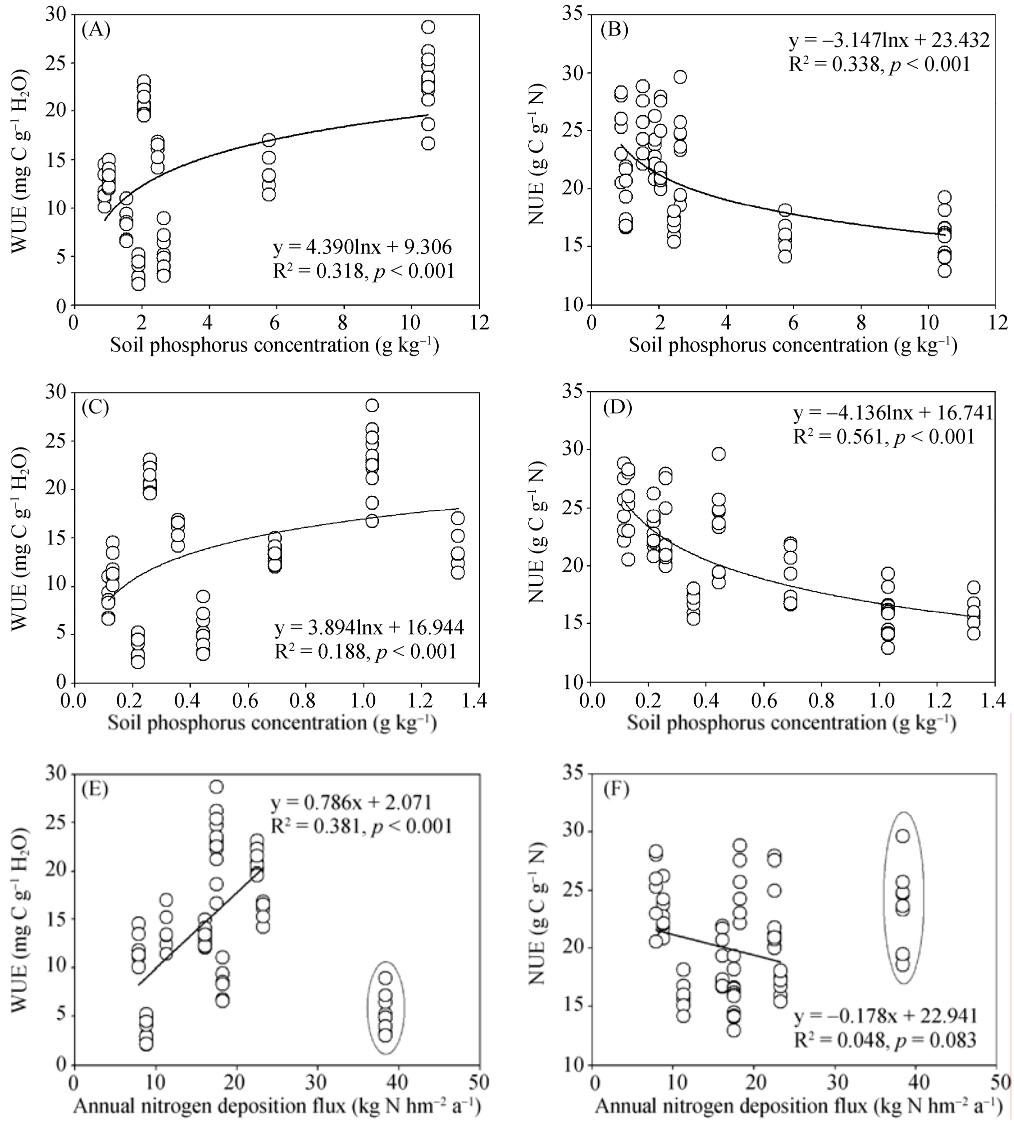

Figure 6 Relationship between WUE/NUE and nutrient factors

The forest ecosystem where annual nitrogen deposition flux is above 25 kg N hm^{-2} a^{-1} is considered to be nitrogen saturated. Therefore, the values in the cycle were excluded from regression analysis in E and F.

Table 3 Stepwise regression for the relationship between vegetable resource use efficiency and environmental factors

Dependent variable	Model	R^2	*p* value
Vegetable WUE	WUE = 27.997–0.938·MAT–12.158·SP+0.910·SN	0.755	< 0.001
Vegetable NUE	NUE = 18.252+0.004·MAP–4.710·SP	0.657	< 0.001

MAT: Mean annual temperature; MAP: Mean annual precipitation; SP: Soil phosphorus concentration; SN: Soil nitrogen concentration

3.6 Relationship between vegetable WUE and NUE

Correlation analyses indicated that vegetable WUE was significantly and negatively

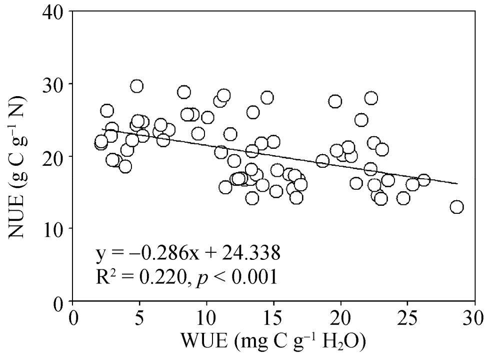

Figure 7 Relationship between vegetable WUE and NUE of predominant species in the typical forest ecosystems along NSTEC

correlated with vegetable NUE in the whole typical forest ecosystems along the NSTEC (p<0.001) (Figure 7), although this relationship was not obvious in any individual forest ecosystem.

4 Discussion

4.1 Climate factors controlling the resource use efficiency

Significant differences in vegetable WUE of predominant species in forest ecosystem along the NSTEC (Figures 3A and 4A) were caused by the large gradient of climate factors. The pattern of vegetable WUE was consistent with the ecosystem WUE obtained by eddy covariance observation (Yu *et al*., 2009), although the absolute value of vegetable WUE was higher. The reason for the difference was that vegetable WUE indicated by foliar δ^{13}C is not equal to the WUE of forest ecosystem, because the former one excludes the water consumption of respiration and soil evaporation (Ebdon *et al*., 1998). Vegetable WUE along the N-STEC was controlled by the distribution of climate factors (Figure 5), which could affect the stomatal conductance. The stomatal conductance decreases under high vapour pressure deficit (VPD), which led to a decrease in intercellular CO_2 concentration. Then it causes an increase in WUE (Anderson *et al*., 2000). However, VPD is strongly controlled by temperature (Keitel *et al*., 2006). That is why WUE was mainly controlled by MAT (Table 3). That the temperature controlled vegetable WUE has been also observed in global vegetable WUE research (Kloeppel *et al*., 1998) through controlled experiment (Craufurd *et al*., 1999), which is employed in vegetation model simulations (Neilson and Drapek, 1998).

NUE decreased from the warm and rainy south to the cold and rainless north along the NSTEC (Figure 4B). Vegetable NUE was significantly correlated with the dominant climate factors (Figures 5B and 5D). The retention of nitrogen within the plant soil system is higher and nitrogen is more tightly conserved in areas with less climatic limitations, because large soil organic carbon, microbial biomass pool and high plant demand for more nitrogen (McCulley *et al*., 2004). Temperature has a more evident impact on plant growth than soil nitrogen mineralization (Wright *et al*., 2004). Thereby, foliar nitrogen would be diluted and vegetable NUE would be increasing as the latitude falling and MAT rising (Figure 5B). Low NUE in cold areas might also reflect the adaptive mechanism which offsets temperature induced reductions in reaction rates and enhances cold hardiness (Kirakosyan *et al*., 2003). The precipitation affects both nutrient availability through influencing microbial activity and nutrient extraction from soils through impacting on plant growth and nutrient demand (Huxman *et al*., 2004). Therefore, MAP was one of the dominant factors impacting the WUE distribution along the NSTEC (Table 3).

4.2 Nutrient status restricting the resource use efficiency

Nutrient status of terrestrial ecosystems has strong local and regional signals due to their acquisition of mineral nutrients mainly via weathering and microbial decomposition at the local sites (Chadwick *et al*. 1999, Liptzin and Seastedt, 2009). A nutrient gradient shows in soil in forest ecosystems along the NSTEC (Table 2). Ordinarily, the effect of soil nutrient on biomass accumulation is weaker than that on foliar nutrient concentration (Birk and Vitousek, 1986). As a result, NUE would descend as the soil nutrient rises from south to north along the NSTEC (Figures 4B, 6B and 6D). However, WUE reflects the compromise between biomass gain and water loss during the growing period and high WUE must have been primarily due to high dry mass production (Livingston *et al*., 1999). Nutrient stimulates photosynthetic rate and accelerated the biomass accumulation, but has little effect on the transpiration rate (Patterson *et al*., 1997). Therefore, vegetable WUE increased in consistent with the increasing of soil nutrient (Figures 6A and 6C). The significant relationship between resources use efficiency and nutrient also indicated that nutrient was the restrict factor of the vegetable growth along the NSTEC. In addition, the correlation coefficients between the resources use efficiency and soil phosphorus were both higher than those between resources use efficiency and soil nitrogen (Figure 6). This result can be supported by the findings of Han (Han *et al*., 2005) that the forest ecosystems along the NSTEC are more limited by soil phosphorus than other parts of the world.

Nitrogen deposition has increased dramatically in recent years (Galloway *et al*., 2004), especially in East China (Lü and Tian, 2007), and has exerted multiple influences on forest ecosystems (Moffat, 1998). Generally, deposited inorganic nitrogen would be held mostly in the forest ecosystems when the nitrogen deposition is below 25 kg N hm^{-2} a^{-1} (Aber *et al*., 1998). However, when the deposition is higher than this level, the carbon and nitrogen cycling would be extremely affected (De Vries *et al*., 2006). In the forest ecosystems along the NSTEC, WUE and NUE also showed anomalous fluctuant versus the general relationship in places where atmospheric inorganic nitrogen deposition is above 25 kg N hm^{-2} a^{-1} (Figures 6E and 6F). This suggests that nitrogen deposition might have saturated in some forest ecosystems along the NSTEC, whose normal biogeochemical cycling would have been disturbed. Moreover, the fluctuant of resource use efficiency might give a signal to those changes.

4.3 A trade-off between NUE and WUE

The significantly negative correlation between vegetable WUE and NUE of predominant species in typical forest ecosystems along the NSTEC revealed that plants with higher WUE would show lower NUE under natural conditions (Figure 7) and vice versa. This result is in accordance with previous studies in both forest and grassland ecosystems (Livingston *et al*., 1999; Chen *et al*., 2005).

Efficient use of resources was very important for growth and survival of forest plants. However, in fact, an increase of use efficiency of one resource would cause a decrease in the efficiency of another. Typically, photosynthetic rate (*A*) of C_3 plants is not saturated with respect to CO_2 (Ehleringer and Pearcy, 1983), but *A* increases with increasing intercellular CO_2 concentration (c_i) (Wong, 1990), which is caused by increasing stomatal conductance (g_s), driven by falling VPD. With no requirement of the investment of additional nitrogen in photosynthetic enzymes, increase in c_i would give rise to the NUE. However, any increase in c_i will also lead to a decrease in WUE based on Eq.3. Therefore, despite decreasing their WUE, plants in wet environment might fully utilize nitrogen resource to maximize their assimilation through gaining per unit of leaf nitrogen. Conversely, plants growing in dry conditions where VPD is high might well underutilize their nitrogen source in order to maximize their WUE. This trade-off is a result of long-term natural selection. The phenomenon also has been found in study conducted in other natural states or control environment in multiple species study (Hirose and Bazzaz, 1998; Li *et al.*, 2007).

5 Conclusions

Based on isotope and stoichiometry analyses of leaf samples from predominant species in the typical forest ecosystems along the NSTEC, this study investigated the distribution and main controlling factors of vegetable WUE and NUE in typical forest ecosystems along the NSTEC. The study addressed some conclusions:

(1) Vegetable WUE ranged from 2.13 to 28.67 mg C g^{-1} H_2O and linearly increased with latitude from south to north, while vegetable NUE showed the opposite trends, decreasing from 29.60 to 12.92 g C g^{-1} N as the latitude increasing.

(2) Vegetable WUE and NUE were determined mainly by climate factors, but also affected by nutrient conditions, especially the soil phosphorus. Mean annual temperature, soil phosphorus concentration, and soil nitrogen concentration were responding for 75.5% of the variations of WUE (p<0.001). While, mean annual precipitation and soil phosphorus concentration could explain 65.7% of the change in vegetable NUE (p<0.001). Atmospheric nitrogen deposition, as an important nutrient resource of forest ecosystems, also impacted vegetable WUE and NUE. In nitrogen saturated forest ecosystems, where annual nitrogen deposition flux was above 25 kg N hm^{-2} a^{-1}, vegetable WUE and NUE were seriously influenced by atmospheric nitrogen deposition.

(3) A trade-off existed between vegetable NUE and WUE in the forest ecosystems along the NSTEC. The trade-off would enable plants to maximize environmental resources in adapting for future global change, by increasing the use efficiency of shortage resource while decreasing the relatively ample one. However, this adaptive mechanism could also be broken off under severe interference, such as heavy nitrogen deposition.

Acknowledgments

We thank the staff working at the nine forest ecosystem observing stations for the helping in the sampling trip. Special thanks go to Dr. WANG Zhenbo for revising the English writing of the manuscript.

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