

A systematic review of research studies on the estimation of net primary productivity in the Three-River Headwater Region, China

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Abstract: The Three-River Headwater Region (TRHR), known as the “Water Tower of China”, is an important ecological shelter for national security interests and regional sustainable development activities for many downstream regions in China and a number of Southeast Asian countries. The TRHR is a high-elevation, cold environment with a unique, but typical alpine vegetation system. Net primary productivity (NPP) is a key vegetation parameter and ecological indicator that can reflect both natural environmental changes and carbon budget levels. Given the unique geographical environment and strategic location of the TRHR, many scholars have estimated NPP of the TRHR by using different methods; however, these estimates vary greatly for a number of reasons. To date, there is no paper that has reviewed and assessed NPP estimation studies conducted in the TRHR. Therefore, in this paper, we (1) summarized the related methods and results of NPP estimation in the TRHR in a systematic review of previous research; (2) discussed the suitability of existing methods for estimating NPP in the TRHR and highlighted the most significant challenges; and (3) assessed the estimated NPP results. Finally, developmental directions of NPP estimation in the TRHR were prospected.

Keywords: Three-River Headwater Region (TRHR); net primary productivity (NPP); estimation methods; NPP models; ecological parameters

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1 Introduction

Vegetation productivity is the basis of energy flow and material circulation in ecosystems (Running, 2012). Researchers from different disciplines have proposed a variety of concepts to describe vegetation productivity. In traditional biomass surveys, accumulation of vegetation production or change in biomass over a specific period is usually used to represent productivity (Lieth, 1973). With the increase in large-scale productivity studies and progress in understanding plant ecophysiological processes, gross primary productivity (GPP) and net primary productivity (NPP) were proposed to represent vegetation productivity (Lieth and Whittaker, 1975; Liu *et al.*, 1997; Zhou and Wang, 2003). Defined as the carbon (or dry matter) fixed by green plants per unit time and space, NPP is closely related to the carbon sink of ecosystems. NPP is also a quantitative measure of the earth’s ability to support life and the ecosystems’ ability to maintain sustainable development. Therefore, NPP has received extensive attention and has become one of the foci of various international research programs (Zhang, 1992; Zhou and Zhang, 1995; Fang *et al.*, 2000).

The Three-River Headwater Region (TRHR), known as the “Water Tower of China”, is the source of the Yangtze, Yellow, and Lancang rivers. Geographically, the TRHR is located in the south of Qinghai Province, ranging from 31°39′–36°16′ N and 89°24′–102°23′ E. The administrative scope of TRHR includes 16 counties in four Tibetan autonomous prefectures (Yushu, Guoluo, Hainan, and Huangnan), as well as the Tanggula town in Golmud City, with an area of approximately $36.3\times10^4\text{ km}^2$ (Figure 1). The TRHR is an important ecological shelter for national security interests and regional sustainable development activities for many downstream regions in China and a number of Southeast Asian countries. However, it is also one of the most vulnerable and sensitive terrestrial ecosystems in China (Qin, 2014). As the hinterland and main body of the world’s “Third Pole”, the TRHR has an average altitude above 4000 m. It has a unique, yet typical alpine vegetation system, and plays an important role in the studies of global change and vegetation’s responses to the change (Liu *et al.*, 2013).

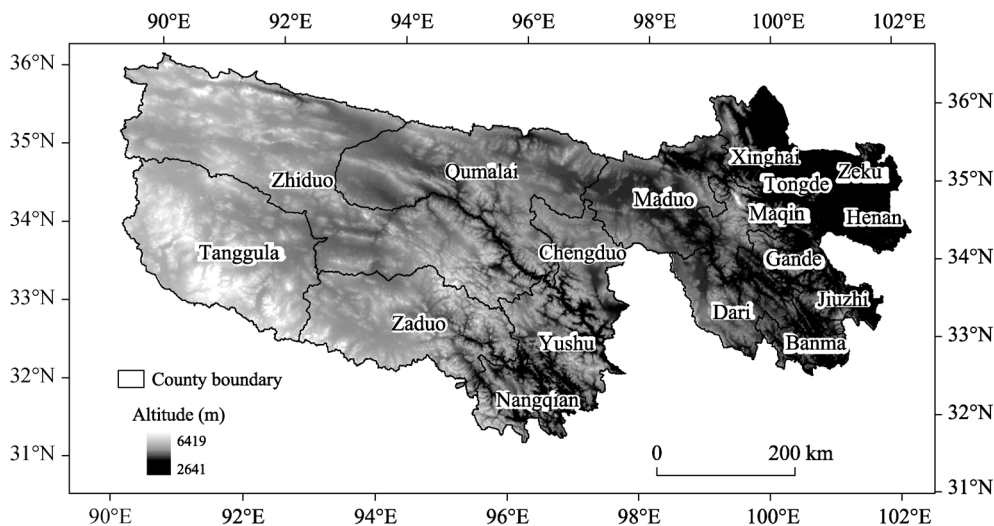


Figure 1 Geographical location and scope of the TRHR

In the past few decades, ecosystems in the TRHR have experienced significant degeneration characterized by grassland degradation, desertification, and an overall reduction in agriculture and animal husbandry production (Li *et al.*, 2004; Tang *et al.*, 2006; Shao *et al.*, 2010). In 2000, Qinghai Province established a provincial nature reserve in the TRHR that has been a national nature reserve since 2003. In 2005, the State Council of China invested 7.5 billion yuan to launch several ecological protection and construction projects in the TRHR, including degraded grassland restoration, local wetland protection, livestock reduction, and management of “black soil beach” (Shao and Fan, 2012). In this context, a comprehensive understanding of the patterns, variation trends, and impact factors of vegetation productivity is pivotal to the policy-making for ecological protection and assessment of ecological engineering in the TRHR.

Although many scholars have applied different methods to estimate NPP in the TRHR, which has effectively promoted research into vegetation productivity and regional carbon accounting, NPP estimation still has many uncertainties and the results vary widely for a variety of reasons. Therefore, based on previous studies, we aimed to systematically summarize the estimation methods and results of NPP in the TRHR. By analyzing these methods, we discuss their suitability and highlight their main challenges when applied to the TRHR. This review also provides an assessment of the existing NPP estimation results. Finally, future developmental directions of NPP estimation in the TRHR are proposed.

2 Estimation methods

Since the late 20th century, many scholars have estimated NPP in the TRHR. The methods they used can be broadly divided into two categories: field measurements and model simulations.

2.1 Field measurements

Field surveys of NPP usually start by measuring plant biomass (Fan, 2003), which includes both aboveground and underground parts of plants. Aboveground NPP is approximately equal to the maximum standing aboveground biomass during one year for deciduous grasses and crops (Luo *et al.*, 2004; Xu, 2010). For evergreen grasses and shrubs, the aboveground biomass needs to be combined with plant longevity to obtain the aboveground NPP. For trees, the aboveground biomass is usually first measured through average sample tree determination or allometry relationships with the observed data, and then the aboveground NPP is further estimated based on the age or growth rate of trees (Zhou and Wang, 2003).

Underground biomass measurements involve full digging, sampling, and ingrowth coring methods. There are three primary methods for estimating underground NPP based on the measurement of underground biomass. The first method directly measures the changes in live root biomass and the losses from decay and animal grazing. While in theory this method provides the closest estimate to the true NPP, taking actual measurements has proven quite difficult (Zhou, 2001). The second method for estimating underground NPP is calculating the difference between the maximum and minimum root biomass during the study period. This method is relatively simple, but it requires multiple measurements of the root biomass (Zhou, 2001). The third strategy, using both underground root biomass and root turnover

fraction to estimate underground NPP, is the most commonly used method (Gill *et al.*, 2002; Zhao, 2009). Besides, with the development of computer technology and image-processing techniques, the minirhizotron is also applied to measure underground NPP. However, this application is currently limited by the relatively high costs and technical requirements for researchers to conduct the measurements.

2.2 Model simulations

NPP models are generally divided into three categories: (1) statistical models (also known as climate-related models), (2) parametric models (also known as light use efficiency (LUE) models), and (3) process models (also known as mechanistic models) (Ruimy *et al.*, 1994; Cramer and Field, 1999; Cramer *et al.*, 1999).

However, with the development of NPP modeling, we believe that this classification may no longer fully and unambiguously summarize the existing NPP models. For example, some statistical models were not based on climate data, but rather utilized remote sensing (RS) vegetation index. Some parametric models were not based on LUE, but referred to climate data instead. RS-process coupled models, which have been widely used, should also be considered and included in the classification. Therefore, NPP models are divided into four categories in this study, according to the primary data used and whether they consider eco-physiological mechanisms: (1) climate models, (2) remote sensing models, (3) process models, and (4) RS-process coupled models.

2.2.1 Climate models

Climate models are driven only by climatic data. As such, simulated NPP using this type of model only reflects potential vegetation productivity (or climatic productivity). According to the existing studies of the TRHR, climate models can be further subdivided into climate-related models, production potential models, and the classification indices model (CIM).

Climate-related models estimate NPP through empirical regression between NPP and climate data, including temperature and precipitation. Guo *et al.* (2013) and Li and Zhang (2014) used the Thornthwaite Memorial model to estimate climatic productivity of the TRHR. Guo *et al.* (2008) used both the Miami and Thornthwaite Memorial models to estimate grassland NPP of Xinghai County in the TRHR.

Production potential models usually reflect combined influences of light, temperature, and water conditions on vegetation productivity. In general, photosynthetic potential productivity is first calculated using solar radiation data. Then, temperature data is applied to revise the photosynthetic potential productivity to obtain the light-temperature potential productivity, which is further revised using precipitation and other climatic data to acquire the climate productivity. For example, Li (2010) used solar radiation, temperature, precipitation, and annual climate change, as well as disaster related data, to obtain the climate productivity of natural grasslands in the TRHR.

The CIM estimates NPP based on the integrated orderly classification system of grassland (IOCSG). The moisture index (K) and $\geq 0^{\circ}\text{C}$ annual average cumulative temperature ($\sum\theta$) are two primary model parameters used in the CIM. NPP is acquired from the specific posi-

tion of the grassland in the IOCSG, which is determined by the two parameters (Lin, 2009). Wang (2013) applied the CIM model to estimate alpine grassland NPP in the TRHR, and concluded that the CIM was more accurate than the climate-related models.

2.2.2 Remote sensing models

Remote sensing models can be divided into statistical models and parametric models according to the calculation methods they use. RS statistical models estimate vegetation productivity based on a variety of vegetation indices. The most commonly used vegetation indices are the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI) (Ma, 2008; Chen *et al.*, 2011; Han, 2015). Studies have shown that NDVI was more suitable for alpine meadow, whereas EVI might be more suitable for alpine steppe (Du *et al.*, 2011).

RS parametric models combine LUE, photosynthetically active radiation (PAR), and fraction of absorbed photosynthetically active radiation (fAPAR) to estimate NPP (Monteith, 1972; Kumar and Monteith, 1981). This type of model is based on the resource balance theory, which indicates that any resource limiting plant growth can be utilized to estimate NPP through conversion factors. RS parametric models utilize PAR, an important limiting resource in photosynthesis, and the concept of LUE to convert absorbed PAR to NPP. RS parametric models, which include CASA (Wu *et al.*, 2011a; Cai *et al.*, 2013; Zhang *et al.*, 2014; Chen, 2015) and GLO-PEM (Xiao *et al.*, 2009; Fan *et al.*, 2010a; Shao and Fan, 2012), are broadly applied in the TRHR.

2.2.3 Process models

Process models differ substantially from the two types of models described above. As the name implies, a process model simulates plant physiological and ecological processes simultaneously with influencing factors and feedback mechanisms. Process models usually consider the soil–plant–atmosphere continuum as an entire system, and often include photosynthesis, respiration, evaporation, transpiration, and stomatal conductance modules. At present, specific applications of process models to estimate NPP in the TRHR have not yet been reported. However, applications have been reported for the Qinghai-Tibet Plateau. Zhou *et al.* (2004), Zhuang *et al.* (2010), and Yan *et al.* (2015) used different versions of TEM to simulate NPP on the Qinghai-Tibet Plateau. Zhang *et al.* (2007) applied CENTURY to estimate vegetation productivity and soil organic carbon on the Plateau. Ye (2010) and Qi *et al.* (2012) utilized Biome-BGC to simulate the temporal variation in NPP on the Qinghai-Tibet Plateau and the impacts of warming on carbon fluxes in an alpine meadow ecosystem, respectively. Concurrently, Piao *et al.* (2012) estimated NPP dynamics of the Qinghai-Tibetan grasslands over the past five decades based on ORCHIDEE. These studies are able to provide a reference for NPP estimation in the TRHR; however, specific quantities and detailed changes in NPP within the TRHR cannot be derived.

2.2.4 RS-process coupled models

RS-process coupled models incorporate the advantages of both process models and RS parametric models and have been gradually developed into an important means of estimating NPP (Feng *et al.*, 2004, 2014). In general, there are two kinds of coupling methods. In the

first method, simplified ecological processes are added to the RS parametric models to enhance the model mechanisms. In the second method, RS techniques are added to the existing process models to address the challenges of model parameterization, error evaluation, and scale transformation faced by most process models.

Wang *et al.* (2009) developed GLOPEM-CEVSA from a RS parametric model, GLOPEM, and a process model, CEVSA, using the first coupling method, and then utilized GLOPEM-CEVSA to estimate the spatio-temporal distribution of NPP in the TRHR. Global MODIS NPP product is also calculated based on a RS-process coupled model (also known as MOD17A3 algorithm). Guo *et al.* (2006) and Zhang *et al.* (2015a) both used MODIS NPP to analyze the spatio-temporal patterns of vegetation productivity in the TRHR. A typical example of the second coupling method is the BEPS model (Liu *et al.*, 1997). BEPS was originally built using the biological principles of the FOREST-BGC with some modifications. The model integrated RS land cover and leaf area index (LAI) to recognize physiological differences among vegetation types and to facilitate scale transformation from leaf level to the whole canopy. Additionally, the model included an advanced canopy radiation sub-model to quantify effects of canopy architecture on the distribution of radiation and photosynthesis in the canopy. Although BEPS model is yet to be applied to the TRHR, its reliability has already been verified in Northern Tibet (Zheng, 2006).

3 Estimated results

At the regional scale, previous studies usually estimated NPP pixel by pixel based on vegetation type, and provided mean NPP of the study area explicitly. Therefore, mean NPP estimates for the entire TRHR were systematically summarized and compared in this study. From Tables 1 and 2, it is evident that mean NPP differs substantially among various studies conducted in the TRHR. For all the vegetation, estimated mean NPP of the TRHR was approximately $258.99 \pm 172.95 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, with the highest NPP of $570.35 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ estimated by Thornthwaite Memorial (Guo *et al.*, 2013) and the lowest NPP of $143.17 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ estimated using GLOPEM-CEVSA (Wang *et al.*, 2009). The highest NPP estimate was approximately four times the lowest NPP estimate. For the grassland, which is the most widely distributed vegetation type in the TRHR accounting for 68% of the total area, simulated mean NPP was approximately $202.65 \pm 129.96 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. The highest grassland NPP estimate was $481.44 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ simulated by Li and Zhang (2014) using Thornthwaite Memorial, and the lowest grassland NPP estimate was $61.42 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ calculated by Wang (2013) using CASA. The former estimate was approximately 7.8 times higher than the latter.

Among different estimation models (Figure 2), climate models produced the highest mean NPP compared with other types of models. Estimated mean NPP of all the vegetation in the TRHR based on climate models was approximately $453.23 \pm 252.30 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, and mean grassland NPP was approximately $283.28 \pm 170.44 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. The second highest estimate was produced using RS models, which estimated mean NPP of all the vegetation in the TRHR to be $165.61 \pm 69.42 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ and mean NPP of grassland to be $147.68 \pm 98.08 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. RS-process coupled models produced the lowest NPP. Estimated mean NPP of

all the vegetation was $143.17 \pm 100.53 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, and mean NPP of grassland was $113.89 \pm 65.57 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

Table 1 Estimated mean NPP of the TRHR in different studies

Study area	Vegetation type	Method & Model	Study period	Mean NPP ($\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)	Reference
TRHR	Grassland	Climate model (Thornthwaite Memorial)	2002–2010	481.44	Li and Zhang, 2014
TRHR	Grassland	Climate model (Production potential model)	1971–2003	225.00	Li, 2010
TRHR	Grassland	Climate model (Miami)	2005–2006	211.92	Wang, 2013
TRHR	Grassland	Climate model (CIM)	2005–2006	214.75	Wang, 2013
TRHR	Grassland	Remote sensing model (CASA)	2005–2006	61.42	Wang, 2013
TRHR	Grassland	RS-process coupled model (MOD17A3)	2005–2006	93.98	Wang, 2013
TRHR	Grassland	RS-process coupled model (MOD17A3)	2000–2010	86.80	Zhang <i>et al.</i> , 2015a
TRHR	All the vegetation	Climate model (Thornthwaite Memorial)	1960–2011	570.35	Guo <i>et al.</i> , 2013
TRHR	All the vegetation	Climate model (Miami)	2004–2008	486.90	Cai <i>et al.</i> , 2013
TRHR	All the vegetation	Climate model (Zhou Guangsheng)	2004–2008	302.45	Cai <i>et al.</i> , 2013
TRHR	All the vegetation	Climate model (CASA)	2001–2010	169.02	Zhang <i>et al.</i> , 2014
TRHR	All the vegetation	Climate model (CASA)	2004–2008	168.68	Cai <i>et al.</i> , 2013
TRHR	All the vegetation	Remote sensing model (CASA)	2010	146.66	Wo <i>et al.</i> , 2014
TRHR	All the vegetation	Remote sensing model (CASA)	2003, 2008, 2013	148.82	Chen, 2015
TRHR	All the vegetation	Remote sensing model (GLOPEM)	1988–2004	194.85	Shao and Fan, 2012
TRHR	All the vegetation	RS-process coupled model (GLOPEM-CEVSA)	1988–2004	143.17	Wang <i>et al.</i> , 2009

Table 2 Estimated mean NPP of different vegetation types in the TRHR

Vegetation type	Mean NPP ($\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)				
	Shao and Fan, 2012	Cai <i>et al.</i> , 2013	Wo <i>et al.</i> , 2014	Wang <i>et al.</i> , 2009	Guo <i>et al.</i> , 2006
Grassland	218.74	/	162.87	160.90	/
Alpine steppe	/	129.41	/	/	79.34
Alpine meadow	/	188.95	/	/	89.38
Forest	405.20	/	279.81	267.90	/
Shrub	156.04	/	/	/	/
Farmland	289.22	/	256.28	222.94	/
Desert	21.48	/	62.81	36.13	/
Marsh	127.09	/	/	161.36	/

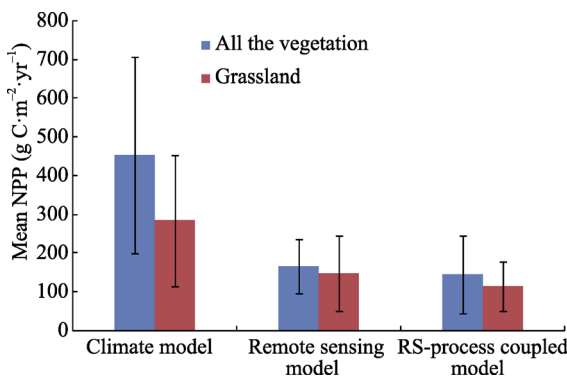


Figure 2 Comparison of estimated NPP based on different models in the TRHR

In general, NPP calculated from climate models was considered as the potential NPP, whereas NPP calculated from other models was considered as the actual NPP. Therefore, it was concluded from NPP estimates that the potential NPP of all the vegetation types in the TRHR was approximately $453.23 \pm 252.30 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, and the actual NPP was $161.87 \pm 63.40 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. The potential NPP of grassland was approximately $283.28 \pm 170.44 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, and the actual NPP of grassland was

$130.79 \pm 73.27 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$.

In terms of different vegetation types, estimated mean NPP displayed the following trend: forest > farmland > grassland > desert (Table 2). Specifically, mean NPP estimates of forest, farmland, grassland, and desert in the TRHR were $317.64 \pm 170.06 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, $256.15 \pm 130.41 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, $130.79 \pm 73.27 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, and $40.14 \pm 25.99 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, respectively. For the grassland, estimated NPP of alpine meadow was generally greater than that of alpine steppe (Guo *et al.*, 2006; Cai *et al.*, 2013), which was also observed in NPP field measurements. Measured NPP of alpine meadow was usually 1–3 times higher than that of alpine steppe (Table 3).

Table 3 Measured grassland NPP at different sites in the TRHR

Site	Latitude	Longitude	Altitude	Vegetation type	Year	Measured NPP(g C·m ⁻² ·yr ⁻¹)	Data source
Zhenqin	N33°24'30"	E97°18'00"	4250 m	Alpine meadow	2010–2011	118.41	Fan, 2003
Wudaoliang	N35°12'56"	E93°04'05"	4626 m	Alpine steppe	2000	53.55	Luo <i>et al.</i> , 2004
Tuotuohe	N34°18'51"	E92°32'52"	4582 m	Alpine steppe	2000	69.30	Luo <i>et al.</i> , 2004
Dawu	N34°23'24"	E100°16'33"	3980 m	Alpine meadow	2014	139.07	Field measurement
Maduo	N34°54'40"	E98°11'13"	4207 m	Alpine steppe	2015	113.23	Field measurement

The original units of NPP in Fan (2003) and Luo *et al.* (2004) were $\text{g DM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and $\text{t DM}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, respectively. We used 0.45 as the C content to convert dry matter (DM) to C to make these results comparable.

4 Evaluation of methods and results

4.1 Estimation methods

Each NPP estimation method has its own advantages and disadvantages. When applied to the TRHR, different estimation methods are confronted by different challenges and suitable for different conditions. As a result, NPP estimates acquired from these methods present different characteristics.

4.1.1 Field measurements

NPP obtained from field measurements is generally believed to be true NPP, and scholars

often refer to the measured NPP as validation for other estimation methods. However, in practice, there are many uncertain factors inherent in field investigations, including (but not limited to) sample selection (whether human activities are present), sample content (whether litter is included), and calculation method (especially the belowground NPP). Differences in these factors can produce varied NPP results. Furthermore, NPP field measurements are mainly based on biomass surveys, so the measured NPP only contains newly produced biomass. Therefore, theoretically, NPP acquired from most field measurements is different from true NPP. The clarification and unification of NPP measuring methods and sampling criteria should become a top research priority (Gao *et al.*, 2012).

4.1.2 Climate model simulations

In general, climate models are only driven by climate data without considering the effects of topography, soil property, availability of nutrients, human activities, and other influencing factors on vegetation productivity. In addition, climate models lack a sound theoretical basis and comprehensive ecophysiological mechanism. Consequently, climate models have low estimation accuracies and produce much larger NPP estimates. According to the estimated results in the TRHR (Table 1), NPP simulated from climate models was usually 2–4 times higher than NPP simulated from other models.

There are two main reasons for such a large difference. Firstly, Miami, Thornthwaite Memorial, and other climate-related models were based on empirical regressions between climatic conditions and measured NPP. Therefore, parameters used in these models may need to be adjusted for a specific region. However, previous studies all applied unadjusted parameters directly to estimate NPP in the TRHR and did not verify the estimated results as the potential NPP could not be verified using the measured NPP. Thus, NPP estimates based on climate models were substantially higher (Guo *et al.*, 2013; Li and Zhang, 2014). The second reason for the significant difference is the fact that the TRHR is a traditional pastoral area. Human management and livestock activities are prominent in the TRHR, and the effects of grazing cannot be ignored; thus, NPP acquired from climate models is significantly different from the actual NPP. Although climate models are relatively simple and convenient to use, they tend to be rather limited in actual application due to low estimation accuracy.

4.1.3 Remote sensing model simulations

RS statistical models are able to accurately estimate NPP in a relatively small area; however, this type of model has poor universality. These models usually directly convert the scale from samples (ground observations) to pixels (remote sensing images) without considering the scale effect, and use a single regression model for all of the vegetation types. Besides, statistical models rely heavily on the measured NPP. These all greatly limit the application of RS statistical models to large-scale NPP studies (Gao *et al.*, 2012).

RS parametric models are commonly used in the TRHR and can provide relatively high estimation accuracies (Shao and Fan, 2012). However, there are still many uncertainties in RS parametric models that need to be highlighted during NPP estimation (Zhang *et al.*, 2011):

(1) As an important input of most RS parametric models, NDVI greatly affects the accuracy of NPP estimation. According to the previous studies (Yang and Piao, 2006; Zhang *et al.*, 2013), NDVI cannot accurately reflect the actual state of vegetation growth when the

coverage of vegetation is very low. In fact, snow, glaciers, bare soils, and rocks, as well as sparse vegetation, are widely distributed in the TRHR, especially in the western part, so the accuracy of remote-sensed NDVI data cannot be guaranteed. In addition, to overcome the interferences of clouds and cloud-shadows, the maximum-value composite (MVC) procedure is often used to produce composite NDVI images. Since the composite NDVI reflects the most optimal vegetation growth state during composite period, instead of the average growth state, this could lead to overestimation of NPP.

(2) Under low temperature conditions, model responses need to be evaluated in relation to the actual situations of the TRHR. For example, in the CASA model monthly NPP is equal to zero when the monthly mean temperature is below -10°C , and the soil water content remains unchanged and the same as in the previous month if the monthly mean temperature falls below 0°C (Zhou and Wang, 2003). However, grasslands in the TRHR are dominated by perennial, deciduous grasses. The aboveground part of grasses is shed annually to avoid the harsh winter, but the perennial underground part is still living. For the trees and shrubs in the TRHR, the aboveground part is partially alive in the winter. Thus, under low temperature conditions, GPP of the TRHR should be equal to zero and NPP should be negative. The treatment of setting NPP to zero in non-growing seasons causes NPP to be overestimated. In addition, it is soil temperature, not atmospheric temperature, that directly influences the soil moisture state. Even if the soil temperature drops below 0°C and the soil begins to freeze, the soil water content will decline significantly before it becomes stabilized (i.e., soil water is completely frozen), and therefore not remain the same as in the previous month.

(3) Models are not able to simulate the detailed changes in processes of NPP. As RS images only record instantaneous values, RS models are only able to estimate limited frequencies of NPP determined by the temporal resolution of RS input data. As a result, RS models can neither provide the detailed changes in processes of NPP, nor identify the key drivers of NPP changes or quantify the human impacts on NPP. In cases where the environment changes rapidly (such as heavy snowfall, outbreaks of pests and diseases, etc.), the reliability of RS models reduces substantially.

Despite the above-mentioned limitations, RS models are able to obtain relatively high estimation accuracies and calculation efficiencies at low costs. RS models are suitable for studies aimed at estimating vegetation standing biomass and its rate of change.

4.1.4 Process model simulations

As process models are yet to be specifically applied to the TRHR, this study only explores their suitability by analyzing the existing process models. The main challenges faced by process models are as follows:

(1) The phenology modules in the process models require comprehensive verification in the TRHR. Phenology, the timing of plant growth and development, is critical for biomass accumulation. An accurate simulation of phenology is a prerequisite for obtaining unbiased NPP estimates in the TRHR (Hidy *et al.*, 2012). However, phenology models were generally established from data collected in specified areas, and did not work well when applied to larger spaces or other places. Currently, most process models, such as Biome-BGC, ORCHIDEE, and LPJ, simulate phenology based on empirical or semi-empirical relationships between phenological stages and climate factors. They assume that phenology is gen-

erally controlled by temperature and moisture conditions in the environment, and the moisture is often described using precipitation (Jolly *et al.*, 2005; Tian and Zeng, 2015). However, in the TRHR, although precipitation is not so much at the beginning of the growing season, soil water is sufficient for vegetation growth due to thawing of the widely distributed frozen soil. Simulation results based on the Biome-BGC also indicated that the start day of the growing season was significantly delayed (approximately in June) due to the high threshold of precipitation to start a new growing season in the model (related results are yet to be published).

(2) Most existing process models cannot accurately simulate the growth and litterfall processes of perennial, deciduous grasses. Most process models are able to simulate the basic biogeochemical processes for grasses, but their descriptions for herbaceous plants are too simple. In Biome-BGC, for example, grasses are comprised of only leaves and fine roots that all become litter at the end of the growing season. The regeneration and litterfall processes of perennial plants are usually controlled by user-defined or default turnover fractions in process models, and the senescence and litterfall processes are generally not considered separately, but dealt with as a single process. If process models are applied directly to estimate NPP in the TRHR without any modification, there is a strong possibility that carbon, nitrogen, and water cycles between different components of plants are simulated inadequately due to the coarse description of grasses. Since vegetation in the TRHR is dominated by perennial plants, the roots do not all die at the same rate and the underground perennial portion remains alive during the winter. Therefore, living and dead roots need to be distinguished, and turnover fractions of the underground fast-cycling portion and the perennial portion should be defined separately in process models, otherwise simulations of root development, soil respiration, litterfall, decomposition, and plant regeneration processes will all be affected, which will definitely impact NPP estimation.

(3) In general, hydrological simulations based on NPP process models are less than ideal. In the TRHR, frozen soils, including permafrost and seasonally frozen soil, are widespread and the thickness of the active layer varies greatly over time. Except for precipitation, underground ice melting and lateral flow are also important sources of soil water. However, most NPP process models have not yet adequately considered the impacts of frozen soils on hydrological processes. Precipitation is considered as the sole source of soil water, and the infiltration depth of precipitation is often set to a constant. These would lead to large simulation errors of soil water content, and further influence the calculation processes of soil evaporation, stomatal conductance, photosynthesis, and transpiration.

(4) Influences of human activities are usually modeled in a very simple manner and not spatially related. Most NPP process models, such as DLEM (Tian *et al.*, 2010), CENTURY (Zhang *et al.*, 2015b), and Biome-BGC (White *et al.*, 2000) use simplified modules or just several parameters to reflect the impacts of human activities on biogeochemical processes. Currently, these models generally have no capacity to account for detailed spatial differences in their simulated results as human activities are not easily spatialized, so the practical applications of NPP process models to ecosystem management and planning are very limited.

(5) No process models have considered the impacts of wildlife on NPP. As a national nature reserve, there are various types and large numbers of wild animals living in the TRHR, including *Pantholops hodgsonii*, *Procapra picticaudata*, *Equus kiang*, and *Procapra prze-*

przewalskii. In order to accurately simulate NPP in the TRHR, impacts of wild animals cannot be ignored.

Simulation accuracies of process models are not necessarily better than those of RS models (Gao *et al.*, 2012). However, as process models can simulate plant physiological and ecological processes as well as the interactions and feedbacks within ecosystems, they are of more significance in the ecosystem management and early-warning analyses.

4.1.5 RS-process coupled model simulations

RS-process coupled models have strengthened the mechanisms behind some processes in RS models, and simultaneously have made the model parameterization and scale transformation in process models easier and more convenient. Although the GLOPEM-CEVSA model proposed by Wang *et al.* (2009) does not use a mechanistic model of photosynthesis, it simulates biomass allocation, respiration, litterfall, and decomposition processes within sound theoretical frameworks. GLOPEM-CEVSA has been well verified in the TRHR. Another RS-process coupled model, the MOD17A3 algorithm, calculates GPP based on a RS parametric model, and estimates autotrophic respiration from mechanisms. The estimated GPP and autotrophic respiration are then combined to obtain NPP (Running and Zhao, 2015). Although there have been a number of studies using the MODIS NPP product in the TRHR (Guo *et al.*, 2006; Zhang *et al.*, 2015a), there are few reports of the accuracy of the MODIS NPP product or MOD17A3 algorithm based on field verifications in the TRHR.

For the difficulties of large-scale phenology simulation, RS-process coupled models have provided effective solutions. For example, the RS-process coupled model, SiB2, utilizes continuous NDVI data to acquire phenological information (Sellers *et al.*, 1996). BEPS model uses LAI data obtained every eight days to reflect phenological changes in vegetation (Sun *et al.*, 2015). Similar to RS models, RS-process coupled models have deficiencies in providing forecasts and early warnings.

4.2 Parameter values

Many parameters used in NPP estimation methods have clear ecological significance. However, in real estimation processes, if the value of a certain parameter deviates wildly, a seemingly accurate result can still be produced by adjusting other parameters. In this case, NPP estimation becomes a purely mathematical game rather than a beneficial insight into mechanisms and changes in the ecosystem. Therefore, utilization of realistic and accurate parameters in the NPP estimation processes does have a significant impact on the development of NPP models and understanding of ecological environments. For brevity, this paper only covers some key parameters used in the processes of NPP estimation. Parameters discussed include the maximum LUE, ratio of underground biomass to aboveground biomass, ratio of live root biomass to total underground biomass, C content, and root turnover fraction.

4.2.1 Maximum light use efficiency

RS parametric models are the most commonly used models for NPP estimation in the TRHR. As an extremely important parameter in RS parametric models, values of the maximum LUE greatly affect NPP estimates. Potter *et al.* (1993) calculated the maximum LUE for global

vegetation as $0.389 \text{ g C} \cdot \text{MJ}^{-1}$; however, many studies have shown that this value was not suitable for the vegetation in China (Zhu *et al.*, 2006). Running *et al.* (2000) used Biome-BGC to simulate values of the maximum LUE for different vegetation types worldwide. Wang (2013) and Wu *et al.* (2011) applied the result for grasslands ($0.608 \text{ g C} \cdot \text{MJ}^{-1}$) from Running *et al.* (2000) to estimate NPP of the TRHR. Zhu *et al.* (2006) simulated values of the maximum LUE for typical vegetation types in China at a national scale, and the values for grasslands/farmlands, forests, and shrubs were found to be $0.542 \text{ g C} \cdot \text{MJ}^{-1}$, $0.389\text{--}0.985 \text{ g C} \cdot \text{MJ}^{-1}$ (considering the differences between coniferous, broadleaf, and mixed forest types), and $0.429 \text{ g C} \cdot \text{MJ}^{-1}$, respectively. Cai *et al.* (2013) directly used these results to simulate NPP of the TRHR. For the Qinghai Province, however, Wei and Wang (2010) calculated the maximum LUE to be only $0.649\text{--}0.908 \text{ g C} \cdot \text{MJ}^{-1}$, $0.114\text{--}0.538 \text{ g C} \cdot \text{MJ}^{-1}$, and $0.115\text{--}0.326 \text{ g C} \cdot \text{MJ}^{-1}$ for forests, shrubs, and grasslands, respectively.

Although the TRHR is subjected to intense solar radiation due to its high altitude, the energy fixed by photosynthesis is limited. Species of plant on the plateau have lower photosynthetic rates and quantum efficiency, as well as lower LUE, than those for the same species on the plain (Zhou, 2001). The direct application of the maximum LUE suitable for global or other areas to the TRHR might lead to an overestimation of NPP. This review suggests that, when estimating NPP in the TRHR, suitable values of the maximum LUE for grasslands, forests, and shrubs should be $0.115\text{--}0.326 \text{ g C} \cdot \text{MJ}^{-1}$, $0.389\text{--}0.908 \text{ g C} \cdot \text{MJ}^{-1}$, and $0.114\text{--}0.538 \text{ g C} \cdot \text{MJ}^{-1}$, respectively.

4.2.2 Ratio of underground biomass to aboveground biomass

To obtain NPP from field measurements, biomass needs to be measured first in most cases. Because aboveground biomass is relatively easy to measure, and direct access to underground biomass is difficult, many scholars have utilized the ratio of underground biomass to aboveground biomass (i.e., root to shoot, R/S) to estimate plant underground biomass. The R/S ratio is commonly adopted in NPP estimation processes, particularly for grasslands. In this article, some results of R/S ratios for primary grassland types in the TRHR are summarized in Table 4, which shows that R/S ratios vary substantially among different studies. Although the R/S ratio carries a certain degree of uncertainty, most studies showed that for alpine meadow and alpine steppe, there was a good correlation between aboveground biomass and underground biomass, and R/S ratios fell within a certain range of variation. Therefore, utilization of R/S ratios to estimate grassland biomass and productivity in the TRHR remains a reliable approach (Ma *et al.*, 2014). According to the field data obtained by

Table 4 Root to shoot (R/S) ratios of primary grassland types in the TRHR

Alpine meadow	Alpine steppe	Temperate steppe	Marsh	Reference	Acquisition mode
4.15	/	/	/	Fan, 2003	Field measurement
6.8	5.2	/	/	Yang <i>et al.</i> , 2009	Field measurement
7.92	4.42	4.32	/	Luo <i>et al.</i> , 2002	Field measurement
7.92	4.25	4.25	15.68	Piao <i>et al.</i> , 2004	Literature review
9.19	9.49	9.19	/	Wang <i>et al.</i> , 2008	Literature review
6.5	6.2	6.4	/	Ma <i>et al.</i> , 2014	Literature review

Yang *et al.* (2009), variation ranges of R/S ratios for alpine meadow and alpine steppe were 0.8–13 and 1.4–12.7, respectively. For the entire alpine grasslands on the Qinghai-Tibet Plateau, the median R/S ratio was approximately 5.8, which was greater than that of the global grasslands.

4.2.3 Ratio of live root biomass to total underground biomass

Only live roots are relevant to vegetation productivity. Thus, when estimating underground NPP in the field measurements, there is a need to distinguish between live and dead roots. The distinction is made subjectively, using color, density, and shape of the roots as distinguishing characteristics. Live roots are usually white or brown in color, whereas dead roots are often black. When roots are placed in water, denser roots sink to the bottom, usually indicating dead roots. In contrast, live roots tend to float. Furthermore, intact roots with a smooth appearance tend to be alive, whereas roots with shredded or folded skin tend to be dead.

Zhou (2001) conducted continuous observations of underground biomass in an alpine meadow ecosystem at Haibei station from May to September between 1980 and 1982, and found that the live root biomass was approximately 70%–80% of the total underground biomass. Fan *et al.* (2010b) assumed the ratio of live root biomass to total underground biomass to be 0.79 during their estimation of grassland NPP in the TRHR. However, according to our measured (unpublished) data obtained in the years of 2005, 2008, and 2015, this ratio was approximately 0.2–0.4 for most sampling sites within the TRHR, and only at some sites in alpine swamp meadow did the ratio exceed 0.6. A good explanation for such a significant difference between these findings has yet to be determined. Possible explanations include different methods used to distinguish between live and dead roots and global climate change, which has significantly increased soil temperatures and decreased soil water content and consequently restricted root longevity compared to that measured in the 1980s.

4.2.4 C content

Calculations of NPP based on biomass require the C content when NPP needs to be expressed as C per unit time and space. Studies by Zhou (2001) and Zhao (2009) showed that C content of plants in the alpine *Kobresia humilis* Serg meadow ranged between 34% and 38%. Research by Chang (2008) carried out in the *Stipa purpurea* alpine steppe revealed that the C content was between 21% and 39% (with an average of 29%). Based on both previously published data and field measurements, Zheng *et al.* (2007) reported that the average C contents of trees, shrubs, and herbs were 46.22%, 45.93%, and 37.13%, respectively, and in herbaceous plants, average C contents of leaves, stems, and roots were 36.83%, 32.57%, and 34.16%, respectively. The C contents of herbaceous plants obtained from aforementioned studies were much lower than the commonly used range of 45%–50%. However, most studies of grassland NPP estimation in the TRHR have assumed 0.45 as the C content (Fan, 2003; Zhang *et al.*, 2015a), which has caused an overestimation of NPP. Therefore, for herbaceous plants in the TRHR, the C content should not exceed 40% in NPP estimation processes, whereas for forests and shrubs, the range of 45%–50% can be used.

4.2.5 Root turnover fraction

Root turnover fraction is defined as the proportion of root production or mortality during a

certain period to the total root biomass (usually one year). A direct measurement of root turnover fraction has proven rather difficult. Gill *et al.* (2002) recommended three ways to estimate the root turnover fraction of grasslands. These include: (1) using the ratio of underground NPP to underground average, minimum, or maximum biomass to acquire root turnover fraction; (2) establishing the empirical relationship between root turnover fraction and aboveground NPP or climate data; and (3) assuming root turnover fraction as a constant value. Fan *et al.* (2010b) utilized the empirical relationship between root turnover fraction and aboveground NPP developed by Gill *et al.* (2002) to estimate root turnover fraction and NPP in the TRHR. In wetlands and marsh areas, they estimated root turnover fraction could exceed 0.7 using this method. In process models, however, constant root turnover fractions are usually used for different vegetation types. Gill *et al.* (2002) proposed that the root turnover fraction of global grasslands was approximately 0.65. Wu *et al.* (2014) applied sequential coring, ingrowth cores, and a minirhizotron to investigate the root production and turnover fraction of grasses in an alpine meadow. The results indicated that different methods could produce very different root turnover fractions, and reliable values ranged between 0.29 and 0.63. Therefore, in estimation processes of grassland NPP in the TRHR, we recommend root turnover fraction should be between 0.29 and 0.65 (Wu *et al.*, 2011b). For wetlands and alpine swamp meadows, the root turnover fraction can be above 0.7 (Zhou, 2001; Fan *et al.*, 2010a).

4.3 Estimated results

4.3.1 Model accuracy

There are several studies evaluating the estimation accuracy of different NPP models. Cai *et al.* (2013) performed correlation analysis between CASA-modeled NPP and measured NPP in the TRHR, and showed that the estimation accuracy of CASA was relatively ideal with the correlation coefficient reaching 0.8. In addition, Cai *et al.* (2013) compared NPP estimates of the CASA model with those of the Miami and Zhou Guangsheng models, and indicated that the latter produced higher estimates with lower accuracies. Fan *et al.* (2010b) calculated NPP and grassland yield based on GLO-PEM model, and verified the simulated yield with the measured yield at the same sites in the TRHR. The results indicated a good correlation between them ($R^2 = 0.54$, $P < 0.01$). In addition, Wang (2013) used the correlation coefficient (r), determination coefficient (R^2), and root mean square error (RMSE) as indicators to evaluate the estimation accuracies of different NPP models based on NPP measurements. Results showed that the performance of MOD17A3 algorithm was most accurate, followed by CASA model, while the Miami and CIM models were least accurate. Therefore, according to the existing evaluation results in the TRHR, RS-process coupled models generally have the best estimation accuracy, followed by RS models, and climate models display the lowest accuracy.

4.3.2 Verification methods

There are four main types of verification methods used in NPP estimation studies of the TRHR: (1) Biomass or grassland yield is obtained and converted to NPP, which is then compared with the simulated results (Cai *et al.*, 2013; Wang, 2013); (2) simulated grassland NPP is first converted to grassland yield and then compared to the investigated yield data

(Wang *et al.*, 2009; Fan *et al.*, 2010b); (3) simulated NPP is compared with the results from previous studies in the same (or a similar) region (Zhang *et al.*, 2014; Chen, 2015); and (4) direct comparisons are conducted using MODIS NPP products (Wo *et al.*, 2014). In terms of NPP verification, two issues require additional attention. First, field data of underground NPP, which is the primary component of total NPP in the TRHR, is extremely underrepresented compared to aboveground NPP. Currently, underground NPP is primarily obtained from conversions of the aboveground biomass or aboveground NPP. However, different studies use various parameter values in conversion processes including R/S ratio, root turnover fraction, and C content, all of which can affect the estimates of NPP. The second is that only the final simulated NPP is actually verified. Intermediate variables are not verified nor do they receive adequate attention. Since only the NPP is verified, estimation processes become “black boxes” in which model applications are little more than “games of parameter adjustment”. If only NPP is correct and intermediate outputs are largely erroneous, this will introduce great uncertainty into ecosystem simulations and early-warning analyses.

4.3.3 Evaluation of results

According to Chapin III *et al.* (2002), NPP includes the new biomass produced by plants, the soluble organic compounds that are diffused or secreted by roots, the carbon transferred into microbes that are symbiotically associated with roots (nitrogen-fixing bacteria and mycorrhizae), losses to herbivory and mortality, and the volatile emissions that are lost from leaves to the atmosphere. Most field measurements of NPP document only the newly produced plant biomass and therefore probably underestimate the true NPP. According to Chapin III *et al.* (2002), only the NPP involved in root secretions accounts for more than 20% of the true NPP.

The TRHR has always been a traditional pastureland. Based on years of foraging surveys and sampling, the annual intake of livestock accounts for approximately 41.48% of grassland aboveground NPP (Zhou, 2001). NPP consumed by wild animals is also significant. In 2013, according to preliminary statistics, there were more than 200,000 wild animals inhabiting Mado County alone, including *Pantholops hodgsonii*, *Procapra picticaudata*, *Equus kiang*, and *Procapra przewalskii*, which greatly exceed the current livestock numbers (about 130,000). The consumption of a *Pantholops hodgsonii* is equivalent to that of six domestic sheep (Song, 2013). In addition, rodents have become a serious problem in some areas of the TRHR (Shao and Fan, 2012). According to conservative estimates, a medium level of rodent density would result in 20%–30% consumption of available livestock pastures (Zhou, 2001). Therefore, a considerable proportion of biomass has already been consumed by herbivores before it can be measured, so even the new biomass measured in field studies is an underestimate of biomass production.

Assuming that the ratio of aboveground NPP to underground NPP for alpine grasslands in the TRHR is approximately 1:2 (Zhou, 2001; Luo *et al.*, 2004), aboveground NPP accounts for approximately 30% of the total NPP. Livestock grazing consumes approximately 12% of the total NPP. Consumption by wild animals is no less than that of the livestock, so it is also estimated at 12% of the total NPP. Intake by rodents is calculated as 20% of livestock consumption, and thus, accounts for approximately 2% of the total NPP. Root secretions are assumed to comprise approximately 20% of the total NPP. Therefore, in summary, most of

the NPP obtained from field measurements in the TRHR might have underestimated the true NPP by at least 40%. If models do not include or cannot reflect these factors causing NPP underestimation, but rather directly take the underestimated NPP as the true NPP in the simulation processes (mainly via parameter calibration and result verification), the estimated NPP based on these models will also be underestimated. Therefore, during NPP estimation processes, the content of simulated NPP and measured NPP must be consistent.

5 Conclusions

The main conclusions of this study can be summarized as follows:

(1) NPP estimation methods can be broadly divided into two categories: field measurements and model simulations. NPP models include climate models, RS models, process models, and RS-process coupled models. The NPP obtained from field measurements is generally considered as the true NPP, and it is often applied to validate the results of other NPP estimation methods. Among different NPP models, RS-process coupled models are generally most accurate, followed by RS models, while climate models are least accurate.

(2) The potential NPP of all the vegetation in the TRHR was approximately $453.23 \pm 252.30 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, and the actual NPP was $161.87 \pm 63.40 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. The potential NPP of grassland was approximately $283.28 \pm 170.44 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, and the actual NPP was $130.79 \pm 73.27 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. Across different vegetation types, estimated mean NPP displayed the following trend: forest > farmland > grassland > desert.

(3) NPP simulated from climate models was usually 2–4 times higher than NPP simulated from other estimation models. Although RS parametric models are commonly used in the TRHR and provide relatively high estimation accuracies, there are still many uncertainties that should be highlighted during NPP estimation. Because of the particular alpine environments, most of the current process models cannot be directly applied to estimate NPP in the TRHR. Additionally, although RS-process coupled models can compensate for some weaknesses of RS and process models, they still have deficiencies in providing forecasts and early warnings.

(4) Most NPP studies have overestimated the maximum LUE for grasslands in the TRHR. The applied ratio of underground biomass to aboveground biomass (R/S ratio) varied substantially among different studies. The assumed ratio of live root biomass to total underground biomass was relatively high, and the measured ratio ranged from 20% to 40%. The C content of herbaceous plants in the TRHR was much lower than the commonly used range of 45%–50%. Recommended root turnover fraction in the TRHR was between 0.29 and 0.65, whereas for wetlands and alpine swamp meadows, root turnover fraction can be above 0.7.

(5) At present, validation for NPP estimates is not comprehensive, and it needs more effort and in-depth research involving the verification method and content. According to preliminary estimates, currently most of the NPP obtained from field measurements in the TRHR might have underestimated the true NPP by at least 40%. If models directly consider the underestimated NPP as the true NPP in the modeling and calculation processes, the estimated NPP will also be underestimated. Therefore, simulated NPP and measured NPP must be consistent in meaning during NPP estimation processes.

6 Outlook

(1) An overall strengthening of data infrastructure in the TRHR is required. Because of the harsh natural environments, fixed and semi-fixed sampling plots, ecological research stations, and micrometeorological tower sites are far from adequate and are distributed unevenly in the TRHR. Furthermore, long-term and systematic observations are severely lacking, and important ecological data including climate, vegetation, soil, and hydrology generally have coarse resolution and bad currency. These all contribute to the challenges of dynamic and unbiased NPP estimation. In recent years, a great deal of money and technology has been invested in the TRHR to construct a network of ecological monitoring stations based on the requirements of ecological protection and construction. These stations on the ground, combined with satellites, have formed a preliminary air-ground environmental monitoring system. It is hoped that, based on this preliminary system, ecological and environmental monitoring in the TRHR can be performed under stable procedures in the future to complete the tasks of data collection and sharing.

(2) An emphasis on the development of process models applicable to the TRHR is required. Process models can be used not only to estimate NPP but also to describe and forecast changes in NPP. However, most existing process models are not capable of accurately simulating the unique ecological processes in alpine environments of the TRHR. Therefore, there is an urgent need to develop NPP process models that can accurately simulate the phenological changes, regeneration, and litterfall processes of perennial, deciduous grasses, presence of the permafrost, and impacts of frozen soil on the water cycle in the TRHR. Furthermore, as the TRHR covers such a wide area, substantial ecological variation has been observed. The spatial differences within the TRHR should be taken into consideration during model development and simulation processes.

(3) The development of NPP models that can depict human activities and wildlife impacts is required. Of all the various NPP models, climate models describe no effects of disturbance factors other than climate change. While RS models can reflect human activities and wildlife impacts in the results, they cannot simulate the impact processes nor can they quantify the degree of influences. Although process models and RS-process coupled models are able to simulate the influences of both human and wildlife activities on NPP estimation, the relevant modules within them are relatively simple, and there has been almost no consideration of wild animals. As a national nature reserve, wildlife numbers in the TRHR have rapidly increased over the years, and it is likely that human activities will also increase with the establishment of national parks in the area. Therefore, it is crucial for the TRHR to develop NPP models that include both human activities and wildlife impacts.

(4) The development of an easy operating platform to run regional-scale models is required. There are a number of models for NPP estimation; however, the actual application of these models to the TRHR at the regional scale might be challenging for scientific researchers or technical staff due to the complexities of the models and laborious tasks of data preparation. These difficulties have greatly limited both the breadth and depth of NPP applications. Therefore, developing an easy operating platform to run regional-scale NPP models deserves high priority.

(5) A convergence of NPP estimates with environmental management practices is also

required. NPP not only reflects the growth state of vegetation but also serves as an important indicator of ecosystem health. Changes in NPP directly affect ecosystem processes and functions that have a profound impact on ecosystem services, which ultimately influences the wellbeing of human populations. Therefore, linking NPP estimation to ecosystem carbon trading, ecological assets valuation, conservation strategy simulation, and other environmental management practices is important for the promotion of NPP studies in the TRHR.

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