Water-Use Efficiency of the Terrestrial Biosphere: A Model Analysis Focusing on Interactions between the Global Carbon and Water Cycles

Akihiko Ito
Center for Global Environmental Research, National Institute for Environmental Studies, Tsukuba, and Japan
Agency for Marine-Earth Science and Technology, Yokohama, Japan

Motoko Inatomi
Japan Agency for Marine-Earth Science and Technology, Yokohama, Japan

(Manuscript received 26 November 2010, in final form 17 November 2011)

ABSTRACT

Carbon and water cycles are intimately coupled in terrestrial ecosystems, and water-use efficiency (WUE; carbon gain at the expense of unit water loss) is one of the key parameters of ecohydrology and ecosystem management. In this study, the carbon cycle and water budget of terrestrial ecosystems were simulated using a process-based ecosystem model called Vegetation Integrative Simulator for Trace Gases (VISIT), and WUE was evaluated: WUE_C, defined as gross primary production (GPP) divided by transpiration; and WUE_E, defined as net primary production (NPP) divided by actual evapotranspiration. Total annual WUE_C and WUE_E of the terrestrial biosphere were estimated as 8.0 and 0.92 g C kg^{-1} H_2O, respectively, for the period 1995–2004. Spatially, WUE_C and WUE_E were only weakly correlated. WUE_E ranged from <0.2 g C kg^{-1} H_2O in arid ecosystems to >1.5 g C kg^{-1} H_2O in boreal and alpine ecosystems. The historical simulation implied that biospheric WUE increased from 1901 to 2005 (WUE_C, +7%; WUE_E, +12%) mainly as a result of the augmentation of productivity in parallel with the atmospheric carbon dioxide increase. Country-based analyses indicated that total NPP is largely determined by water availability, and human appropriation of NPP is also related to water resources to a considerable extent. These results have implications for 1) responses of the carbon cycle to the anticipated global hydrological changes, 2) responses of the water budget to changes in the terrestrial carbon cycle, and 3) ecosystem management based on optimized resource use.

1. Introduction

Water-use efficiency (WUE; defined as carbon gain at the cost of unit water loss) is a key parameter for analyzing the metabolism of terrestrial ecosystems—closely related to interactions between the carbon and water cycles at the leaf to watershed scales. For leaf-level WUE, the exchange of both CO_2 and water vapor is coregulated by stomatal aperture (Cowan 1977; Farquhar and Sharkey 1982), whereas ecosystem-level WUE varies among plant functional types and environmental conditions (Jarvis and McNaulton 1986; Schulze et al. 1987). WUE is also related to plant resource use and survival strategies along a gradient of water availability from desert to rain forest, as well as plant responses to changing environments. For agriculture, WUE represents an expected crop yield at the expense of a certain amount of water supply and is important for agronomic crop breeding in dry-land farming and for management of irrigation water.

In the face of global environmental issues such as climatic change and ecosystem degradation, a deeper understanding of the carbon and water cycles is necessary for appropriate ecosystem management (Chapin et al. 2009; Vorosmarty et al. 2010). This is one of the purposes of ecohydrology (e.g., Rodriguez-Iturbe 2000)—a recently developed field of interdisciplinary research. In addition to leaf-level measurements and inventory surveys, recent advances in micrometeorological flux measurements have provided new data for evaluating the
carbon and water cycles (e.g., Law et al. 2002). However, our understanding of the large-scale processes is still insufficient, and researchers continue to debate the reason for the historical increase of runoff discharge from the land surface: plant stomatal closure caused by elevated atmospheric CO$_2$ (e.g., Gedney et al. 2006) versus land-use change (e.g., Piao et al. 2007).

An improved understanding of WUE would help to resolve these issues, but several hurdles must be overcome. First, different definitions of WUE have been used. At the canopy level, WUE is usually defined as net or gross CO$_2$ assimilation at the cost of water loss by transpiration. However, stand-level WUE is often defined as plant CO$_2$ assimilation at the cost of total water loss by evapotranspiration. This discrepancy makes it difficult to compare WUE values from different sources. Second, WUE has been evaluated at different spatial and temporal scales, ranging from single stomata to the whole biosphere. At landscape and higher scales, the water and carbon cycles occur heterogeneously over the land surface, requiring an appropriate scaling-up methodology. Third, the carbon and water cycles encompass a variety of complicated processes, including wildfire regimes, which are affected by fuel moisture status; soil carbon loss as related to water erosion; and human activities such as deforestation and irrigation.

The primary objective of this study was to simulate and analyze WUE of the global terrestrial ecosystem using a process-based model including major hydrological and biogeochemical processes. Although several model studies have explored the interaction between water and carbon cycles (e.g., Kucharik et al. 2000; Sitch et al. 2003; Krinner et al. 2005; Alton et al. 2009), few global-scale analyses have examined WUE in relation to natural and human factors. Therefore, we investigated WUE on the basis of global simulations in conjunction with ancillary inventory data on human impacts.

2. Methods and data

a. Definition of water-use efficiency

WUE has been defined for different flux components, time periods, and spatial extents. For large-scale analyses, this study focuses chiefly on annual (i.e., summation from January to December) properties and considers two definitions of WUE (g C m$^{-2}$ yr$^{-1}$). WUE$_C$ focuses on canopy-level exchange of H$_2$O and CO$_2$ and is calculated as follows:

$$WUE_C = \frac{GPP}{TR},$$

where GPP is gross photosynthetic (primary) production (g C m$^{-2}$ yr$^{-1}$) and TR is transpiration (kg H$_2$O m$^{-2}$ yr$^{-1}$), both of which are strongly regulated by stomatal aperture. WUE$_S$ focuses on the stand-level carbon cycle and water budget and is calculated as follows:

$$WUE_S = \frac{NPP}{AET},$$

where NPP is net primary production (g C m$^{-2}$ yr$^{-1}$) and AET is actual evapotranspiration, including transpiration and surface evaporation (kg H$_2$O m$^{-2}$ yr$^{-1}$). NPP is an important ecosystem index representing vegetation growth activity, biogeochemical cycles, and ecosystem services such as food and fiber supply (Millennium Ecosystem Assessment 2005). Several different definitions are additionally considered here such as stand flux-based WUE defined as GPP/AET.

b. Model description

A process-based terrestrial ecosystem model, the Vegetation Integrative Simulator for Trace Gases (VISIT; Inatomi et al. 2010; Ito 2011b), was adopted in this study. The model consists of radiation, water, carbon, and nitrogen schemes, which are all mutually linked. The carbon cycle and water budget schemes are based on a simple biogeochemical model, Simulation Model of Carbon Cycle in Land Ecosystems (Sim-CYCLE; Ito and Oikawa 2002), which simulates stand-level processes at a monthly time step and is scalable to broad scales using appropriate mesh data. To explain how the model estimates WUE$_C$ and WUE$_S$, brief descriptions of GPP, NPP, TR, and AET are provided in this section.

NPP (g C m$^{-2}$ yr$^{-1}$) is calculated as the difference between GPP (total photosynthetic CO$_2$ assimilation) and autotrophic plant respiration (AR). GPP is a function of the incident shortwave radiation, canopy leaf area index (LAI; estimated from leaf mass), attenuation coefficient, leaf-level light-use efficiency, and maximum photosynthetic rate. In the model, the attenuation coefficient is a biome-specific parameter (0.3–0.7; Ito and Oikawa 2002). The light-use efficiency and maximum photosynthetic rate are functions of temperature, intercellular CO$_2$ concentration, and soil water content, taking into account biome-specific ecophysiological characteristics (see Table 1 for biome types). For example, GPP by C$_3$ and C$_4$ plants is calculated separately using specific parameter values (for details, see Ito and Oikawa 2002). Intercellular CO$_2$ concentration is estimated from ambient CO$_2$ concentration and stomatal gas conductance, as parameterized by Leuning (1995). AR is composed of growth and maintenance respirations, which are separately estimated for leaves, stems, and roots. The growth respiration rate (the cost to produce a new organ) is proportional to the amount of carbon allocation to each organ, whereas the maintenance...
respiration rate increases linearly with standing biomass and exponentially with temperature.

In the hydrology scheme of the model, AET (kg H2O m⁻² yr⁻¹) is composed of plant TR, evaporation of canopy-intercepted precipitation (EI), and evaporation of soil surface water (ES). WUEC is obtained from Eq. (1), and WUES is estimated by the following:

\[
\text{WUES} = \frac{\text{NPP}}{\text{AET}} = \frac{(\text{GPP} - \text{AR})}{(\text{TR} + \text{EI} + \text{ES})}. \tag{3}
\]

Temporal variation in soil water (ΔSW) is estimated by the water budget equation: ΔSW = PR − AET − RO, where PR is precipitation and RO is runoff discharge. In the model, the upper (0–10-cm depth) and lower (>10 cm to rooting depth) soil water pools are calculated. To estimate actual evapotranspiration (AET = TR + EI + ES), potential evapotranspiration (PET) is estimated by the Penman–Monteith equation (Monteith and Unsworth 1990) for each component. Then, actual EI is obtained by considering the capacity of water interception on the leaf surface (0.125 kg H2O m⁻² leaf area), and actual ES is obtained by considering the limitation of soil water content. In the hydrology scheme, snow water accumulation and its impact on surface reflectance (albedo) are considered.

The major coupling processes between the carbon and water cycles are included in the model: 1) leaf gas exchanges of CO₂ and water vapor are coregulated by stomatal conductance; 2) stomatal conductance is affected by the ambient CO₂ and humidity conditions; 3) soil water content restricts the maximum photosynthetic rate, light-use efficiency, and stomatal conductance; 4) soil water content is affected by plant uptake through transpiration, which is affected by the amount of canopy leaves; 5) water availability affects LAI through limitations on photosynthetic carbon gain; 6) LAI also affects ES by altering net radiation of the soil surface; 7) the decomposition rate is influenced by soil moisture content; and 8) soil carbon stock is affected by soil loss due to water erosion.

The VISIT model has been validated in previous studies. The estimated carbon cycle and water budget have been validated with observational data from 17 sites worldwide (Ito and Oikawa 2002). The estimated gross and net CO₂ fluxes have been compared with tower-based measurement data collected mainly in Asia, confirming that the model reasonably captures temporal and spatial variability (Ito 2008; Inatomi et al. 2010). The simulated regional carbon budget has been compared with those estimated by other models (Ichii et al. 2010), and the findings indicated that the VISIT model provides intermediate estimations. The global results of NPP and

<table>
<thead>
<tr>
<th>Biome</th>
<th>Area (10⁶ km²)</th>
<th>SPP (kg C m⁻² yr⁻¹)</th>
<th>GPP (kg H₂O m⁻² yr⁻¹)</th>
<th>TR (kg H₂O m⁻² yr⁻¹)</th>
<th>EI (kg H₂O m⁻² yr⁻¹)</th>
<th>WUES (g C kg⁻¹ H₂O)</th>
<th>WUEC (g C kg⁻¹ H₂O)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical evergreen forest/woodland</td>
<td>1.5</td>
<td>0.2</td>
<td>12.5</td>
<td>2.4</td>
<td>1.2</td>
<td>0.6</td>
<td>1.24</td>
</tr>
<tr>
<td>Tropical deciduous forest/woodland</td>
<td>15.3</td>
<td>2.3</td>
<td>12.3</td>
<td>1.3</td>
<td>0.9</td>
<td>0.6</td>
<td>1.24</td>
</tr>
<tr>
<td>Temperate deciduous forest/woodland</td>
<td>4.3</td>
<td>1.3</td>
<td>1.32</td>
<td>0.12</td>
<td>0.11</td>
<td>0.04</td>
<td>0.12</td>
</tr>
<tr>
<td>Temperate needleleaf evergreen forest/woodland</td>
<td>2.9</td>
<td>1.0</td>
<td>0.79</td>
<td>0.07</td>
<td>0.06</td>
<td>0.01</td>
<td>0.07</td>
</tr>
<tr>
<td>Boreal evergreen forest/woodland</td>
<td>6.2</td>
<td>0.64</td>
<td>0.43</td>
<td>0.03</td>
<td>0.02</td>
<td>0.01</td>
<td>0.03</td>
</tr>
<tr>
<td>Boreal deciduous forest/woodland</td>
<td>14.2</td>
<td>0.86</td>
<td>0.35</td>
<td>0.08</td>
<td>0.06</td>
<td>0.01</td>
<td>0.06</td>
</tr>
<tr>
<td>Evergreen/deciduous mixed forest/woodland</td>
<td>15.8</td>
<td>0.86</td>
<td>0.31</td>
<td>0.02</td>
<td>0.02</td>
<td>0.01</td>
<td>0.02</td>
</tr>
<tr>
<td>Grassland/steppe</td>
<td>6.1</td>
<td>0.46</td>
<td>0.28</td>
<td>0.01</td>
<td>0.01</td>
<td>0.00</td>
<td>0.01</td>
</tr>
<tr>
<td>Dense shrubland</td>
<td>15.3</td>
<td>0.89</td>
<td>0.46</td>
<td>0.02</td>
<td>0.02</td>
<td>0.01</td>
<td>0.02</td>
</tr>
<tr>
<td>Tundra</td>
<td>7.1</td>
<td>0.5</td>
<td>0.36</td>
<td>0.01</td>
<td>0.01</td>
<td>0.00</td>
<td>0.01</td>
</tr>
<tr>
<td>Desert</td>
<td>15.1</td>
<td>0.17</td>
<td>0.76</td>
<td>0.04</td>
<td>0.04</td>
<td>0.01</td>
<td>0.04</td>
</tr>
<tr>
<td>Cropland</td>
<td>15.0</td>
<td>0.95</td>
<td>0.65</td>
<td>0.04</td>
<td>0.04</td>
<td>0.01</td>
<td>0.04</td>
</tr>
<tr>
<td>Total</td>
<td>131.3</td>
<td>0.93</td>
<td>0.65</td>
<td>0.44</td>
<td>0.03</td>
<td>0.01</td>
<td>0.04</td>
</tr>
</tbody>
</table>

The WUEC is obtained from Eq. (1), and WUES is estimated by the following:

\[
\text{WUES} = \frac{\text{NPP}}{\text{AET}} = \frac{(\text{GPP} - \text{AR})}{(\text{TR} + \text{EI} + \text{ES})}. \tag{3}
\]
LAI have been compared with observational database and satellite remote sensing data (Hazarika et al. 2005; Kato et al. 2009). Figure 1 shows the latitudinal distributions of runoff ($PR - AET$) and NPP estimated by VISIT, in comparison with representative previous studies: Fekete et al. (2002) for runoff and Cramer et al. (1999) for NPP. The global VISIT simulation reasonably captured the highest peaks of evapotranspiration and productivity at lower latitudes and the second-highest peaks at northern latitudes around 60°N with a vast area of landmass.

**c. Simulation design**

A global simulation experiment using VISIT was conducted at a spatial resolution of $0.5^\circ \times 0.5^\circ$ for latitude and longitude, for the period from 1901 to 2005, at a monthly time step (Ito 2005, 2011b). Before performing the experiment, a spinup calculation was conducted for 300–4000 yr until an equilibrium carbon budget under a stationary climate condition for each grid cell was reached. Actual biome and land-cover distributions were derived from Olson et al. (1983) and Ramankutty and
Foley (1999); in this case, natural vegetation was classified into 15 major biomes (Table 1). Soil conditions such as the sand and clay fractions, field capacity, and bulk density were determined using a global dataset of the International Satellite Land Surface Climatology Project Phase II (Hall et al. 2006). Values for natural ecosystems and croplands were calculated separately in the model. In croplands, planting and harvesting of crops were considered on the basis of a conventional crop calendar (i.e., planting in spring and harvesting in autumn). Note that the amount of water supplied to croplands for irrigation was not explicitly considered in this study (see section 3e for the potential uncertainty and limitations of this study). Historical changes in land use (fractional changes in cropland and pasture) were based on a dataset compiled by Hurrut et al. (2006). The historical climate dataset Climatic Research Unit Time Series version 3.0 (CRU TS3.0) (air temperature, precipitation, cloud cover, and vapor pressure; Mitchell and Jones 2005) was used to drive the model. Historical changes in atmospheric CO2 concentration were prescribed on the basis of observations (Keeling and Whorf 2009).

Most analyses were done for a baseline simulation conducted using a default parameter set (Ito 2011b). Additionally, when analyzing interannual variability and linear trends, parameter-induced uncertainty was considered by introducing perturbation terms into model parameters (e.g., maximum photosynthetic rate and respiratory temperature dependence). Ensemble simulations were conducted 120 times, in which random values (within ±20%) were chosen and added to the default parameter values. The parameter-perturbed experiment may represent the range of uncertainty and robustness of the analyses.

d. Ancillary inventory data

To examine the impacts of human appropriation such as food harvest and water withdrawal, ancillary inventory data at around 2000 were also used. Haberl et al. (2007) estimated the global distribution of human appropriation (consumption for various uses) of NPP (HANPP; fractional intensity). Using the data and natural NPP estimated by VISIT, the amount of HANPP was estimated. To relate WUE to statistical data of human activities, country-based water resource and freshwater withdrawal data were obtained from a hydrological database, AquaStat, of the Food and Agriculture Organization of the United Nations (FAO; http://www.fao.org/).

3. Results and discussion

a. Global terrestrial water-use efficiencies

The global carbon cycle and water budget of terrestrial ecosystems were estimated in the default simulation, as summarized in Fig. 2. The average WUEC and WUES of the terrestrial biosphere around 2000 were estimated as 8.02 ± 0.07 g C kg⁻¹ H₂O and 0.920 ± 0.014 g C kg⁻¹ H₂O (mean ± standard deviation of interannual variability).

The estimated global NPP, 58.3 × 10¹² kg C yr⁻¹, is close to the median value of modern estimates, 56.4 × 10¹² kg C yr⁻¹, based on a meta-analysis for 251 estimates (Ito 2011a). The estimated total AET, 63.5 × 10¹³ kg H₂O yr⁻¹ (10¹³ kg H₂O ≈ 10³ km³ H₂O), is comparable with those of previous studies: 69.6 × 10¹⁵ kg H₂O yr⁻¹ (Postel et al. 1996), 65.5 × 10¹⁵ kg H₂O yr⁻¹ (Oki and Kanae 2006), 62.97 × 10¹⁵ kg H₂O yr⁻¹ (Rost et al. 2008), and 72.1 × 10¹⁵ kg H₂O in 1985–99 (Hanasaki et al. 2010). Of the average AET estimated by the model (an areal average of 483.5 kg H₂O m⁻² yr⁻¹), TR, EI, and ES account for 24.0%, 24.2%, and 51.8%, respectively.

b. Spatial and interbiome variability

The annual water cycle (e.g., AET) and carbon cycle (e.g., NPP) estimated by the model were heterogeneous over the land surface. Higher AET (Fig. 3a) and NPP (Fig. 3b) occurred in tropical rain forests in South America, central Africa, and Southeast Asia. Both AET and NPP decreased in water-limited (e.g., desert) and radiation-limited (e.g., high-latitude tundra) areas. The estimated WUES (Fig. 4) varied ranging from <0.2 g C kg⁻¹ H₂O in deserts of northern and southern Africa, the western United States, Australia, and western and central Asia to >1.5 g C kg⁻¹ H₂O in boreal forests and tundra of North America, Eurasia, and the Tibetan Plateau. Most humid forest ecosystems showed intermediate WUES (0.6–1.2 g C kg⁻¹ H₂O).

Biome-specific water and carbon budgets and WUE values estimated by the model simulation are summarized in Table 1. Arid biomes such as desert and shrub land had higher WUEC values than those in humid environments such as forests [except boreal deciduous (i.e., larch) forest]. In contrast, forest ecosystems had comparable or higher WUES values among the biomes. The difference in WUEC and WUES among biomes implies that the lower WUES (i.e., lower sensitivity of plant production to water conditions) in water-limited ecosystems is mainly attributable to higher water loss by evaporation of soil and canopy-trapped water. It is noteworthy that field studies identified another mechanism explaining lower WUE in water-limited ecosystems—namely, fast transpiration promoting plant growth during the brief humid periods (DeLucia and Schlesinger 1991), which was not included in the present model simulation.

The observed WUE values in previous studies, including data syntheses by Buchmann and Schulze (1999)
and Beer et al. (2009), are summarized in Table 2. The magnitude of WUE estimated by the model (Table 1) is comparable to results of previous field studies (Table 2). For example, the average GPP/AET values estimated by the model for evergreen broadleaf forest, 2.23–2.67 g C kg\(^{-1}\) H\(_2\)O, are comparable with observations: 1.88–6.07 g C kg\(^{-1}\) H\(_2\)O. In grasslands, the model estimated GPP/AET as 0.91–2.37 g C kg\(^{-1}\) H\(_2\)O, and the observed values ranged from 0.41 to 4.35 g C kg\(^{-1}\) H\(_2\)O. Note that the observations may contain a larger range of variability because of limited spatial and temporal representativeness (e.g., <1 km\(^2\) for a few years). The interbiome difference is also consistent with observations. Ponton et al. (2006) compared canopy-scale WUE\(_C\) (GPP/TR) among evergreen needleleaf, deciduous broadleaf, and grassland sites in Canada and found that forests have higher WUE\(_C\) (4–10 mmol CO\(_2\) mol\(^{-1}\) H\(_2\)O) than grasslands (1–4 mmol CO\(_2\) mol\(^{-1}\) H\(_2\)O). However, it is generally difficult to validate the estimated WUE distribution with observational data, mainly because of the lack of direct observation of broad-scale WUE. Dan and Ji (2007) estimated the global distribution of WUE using the Atmosphere–Vegetation Interaction Model (AVIM)–Global Ocean–Atmosphere–Land System Model (GOALS) and found higher WUE values in northern midlatitude ecosystems—a finding that is consistent with the present study. Tian et al. (2010) constructed a map of WUE\(_S\) (NPP/AET) estimated by the Dynamic Land Ecosystem Model in the southeastern United States. An east–west difference in WUE\(_S\) along a humidity gradient was evident, ranging from <0.4 g C kg\(^{-1}\) H\(_2\)O in western inland regions to 1.0–1.3 g C kg\(^{-1}\) H\(_2\)O in the eastern Atlantic coastal region; this tendency was properly captured by the VISIT simulation in this study. Using field data measured along grassland transects in China, Hu et al. (2010) showed that dryer grasslands exhibited lower precipitation-use efficiency (defined as above-ground NPP/precipitation). Beer et al. (2007) estimated the distribution of WUE (defined as GPP/AET) for Europe, and they found a latitudinal gradient, with higher values in northern Europe and lower values in the Mediterranean region. These spatial gradients were
largely captured by the WUE gradient based on NPP in this study.

c. Temporal variability

The historical simulation indicated that global total WUE increased gradually during the last century (Fig. 5). The estimated average WUE_c increased from 7.5 g C kg^{-1} H_2O in 1901–40 to 8.0 g C kg^{-1} H_2O in 1995–2004 (Fig. 5e), and the estimated average WUE_s increased from 0.82 g C kg^{-1} H_2O in 1901–40 to 0.92 g C kg^{-1} H_2O in 1995–2004 (Fig. 5f). This increment was largely attributable to the increase in photosynthetic carbon uptake (Figs. 5a,b), which compensated for the small increase in water loss (Figs. 5c,d). For example, the estimated average NPP increased from 50.5 \times 10^{12} kg C yr^{-1} in 1901–10 to 58.5 \times 10^{12} kg C yr^{-1} in 1995–2004 (+15.9%), whereas the estimated average AET increased from 61.4 \times 10^{15} kg H_2O yr^{-1} in 1901–10 to 63.6 \times 10^{15} kg H_2O yr^{-1} in 1995–2004 (+3.6%). Such an incremental trend of carbon uptake is consistent with previous historical simulation studies (e.g., Cramer et al. 2001; Piao et al. 2009). Note that 1) both water and carbon cycles are driven largely by solar radiation and precipitation, and variability in the water and carbon processes were significantly correlated even at the global annual scale (GPP versus TR, r^2 = 0.96, p < 0.05; NPP versus AET, r^2 = 0.74, p < 0.05); 2) impacts of disturbances such as land-use change and wildfires on the carbon cycle and water budget were included through the decline in LAI, change in the radiation budget, and carbon release by biomass burning; 3) atmospheric CO_2 concentration increased from 291 ppmv in 1901 to 380 ppmv in 2005, leading to a CO_2 fertilization effect on photosynthetic carbon gain; and 4) the decrease in stomatal aperture due to the elevated CO_2 concentration did not result in a considerable decrease in the total AET (or an increase in total runoff discharge; data not shown) during the experimental period. Indeed, several field studies (e.g., Polley et al. 2002) observed that leaf-level WUE increases linearly with ambient CO_2 level. Consequently, the historical increase and interannual variability in GPP and NPP explains 97% of the temporal variability in WUE at the global scale (Fig. 5).

Physiological and ecohydrological studies revealed that plant WUE is closely related to the stable isotopic composition (i.e., \delta^{13}C) of photosynthate. Using historical tree-ring records and archived specimens, many studies (e.g., Bert et al. 1997; Saurer et al. 2004; Köhler et al. 2010) have reconstructed WUE of terrestrial plants during past decades and centuries. Bert et al. (1997) analyzed tree-ring data from silver fir trees in France and found that intrinsic (i.e., stoma level) WUE increased by 30% in the twentieth century. Saurer et al.
Köhler et al. (2010) analyzed herbage specimen data from England and found that intrinsic WUE has increased by 18%–33% since 1857. Although plant material analyses indicate only leaf stomatal WUE (i.e., carbon loss by stem and root respiration and water loss by evaporation from intercepted water and soil water are not taken into account), these findings strongly support the increase of WUE estimated in this study. Additionally, the WUE$_S$ trend estimated by VISIT is consistent with the regional-scale study by Tian et al. (2010), who reported that ecosystem WUE$_S$ in the southern United States has increased by 25% since 1895. The estimated global WUE accounted for the historical change in cropland area, but did not consider advances in water management practices (see section 3e for the potential uncertainty and limitations of this study).

In the model simulation, average total RO increased from $41.4 \times 10^{15}$ kg H$_2$O yr$^{-1}$ in 1901–40 to $42.0 \times 10^{15}$ kg H$_2$O yr$^{-1}$ in 1995–2004 (+1.7%). Such an incremental trend is qualitatively consistent with field studies (e.g., Labat et al. 2004) and previous model studies (e.g., Gedney et al. 2006; Piao et al. 2007). However, the estimated magnitude of the RO increment was smaller than those of the precipitation (+2.9%) and AET (+3.6%). The finding of Gedney et al. (2006) and Betts et al. (2007) imply that the RO increment is attributable to stomatal response to the elevated ambient CO$_2$ concentration, leading to decreased AET and increased RO through time. In contrast, Piao et al. (2007) conducted a series of simulations using the Organizing Carbon and Hydrology in Dynamic Ecosystems (ORCHIDEE) model and found that the increased RO in the twentieth century was largely attributable to land-use change. Furthermore, Peel and McMahon (2006) called attention to the quality and extrapolation procedure of the runoff record. Although the VISIT simulation of the present study included both stomatal response and land-use change, the estimated RO increment was smaller than those reported in previous studies. In our simulation, the elevated CO$_2$ concentration enhanced photosynthetic production, leading to an expansion of canopy leaf area (except in deforested regions) and an increase in the canopy-scale transpiration (+8.1%; global average) and evaporation of canopy-intercepted precipitation (+11.6%; global average). Further observations and in-depth modeling studies are required to reconcile these inconsistent results.

d. Human dimensions of water-use efficiency

During the experimental period, cropland area increased from $8.3 \times 10^6$ km$^2$ in 1901 to $15.2 \times 10^6$ km$^2$ in
that is, from approximately 5.5% to 10% of the total land area. Thus, human activities have affected the water and carbon cycles and therefore the WUE of the terrestrial biosphere. Figure 6 shows latitudinal distributions of the simulated AET and NPP in 1995–2004. Globally, 14.6% of AET and 12.2% of NPP was from croplands, and total AET of croplands in this period was estimated as 8673 km\(^3\) yr\(^{-1}\). This estimate is consistent with those of previous studies: 7820 km\(^3\) yr\(^{-1}\) for rain-fed cropland and 9540 km\(^3\) yr\(^{-1}\) for all croplands estimated by Hanasaki et al. (2010) using a water-resource model (H08; Hanasaki et al. 2008) and 8501 km\(^3\) yr\(^{-1}\) for all (rain fed + irrigated) croplands estimated by Rost et al. (2008) using a vegetation–cropland model [Lund–Potsdam–Jena managed Land (LPJmL)]. In the present study, we did not separate rain-fed and irrigated croplands or distinguish precipitation-originated (“green water”) from groundwater-originated (“blue water”) AET (Falkenmark and Rockström 2004). Forest ecosystems play major roles in AET and NPP at most latitudes, and croplands made a substantial contribution within a wide range of latitudes, accounting for as much as 26% of total NPP around 36°N. In the model simulation, croplands showed lower WUE (on average, 0.83 g C kg\(^{-1}\) H\(_2\)O; Table 1) than forest ecosystems (on average, 1.10 g C kg\(^{-1}\) H\(_2\)O). Therefore, land-use conversion from forest to cropland can, in general, lower total WUE at broad scales.

According to the model simulation, based on the world average, terrestrial ecosystems provided 9727 kg C yr\(^{-1}\) of NPP to each person around 2000. Using the human appropriation intensity reported by Haberl et al. (2007), the total HANPP was estimated as 12.9 \(\times 10^{12}\) kg C yr\(^{-1}\), or 21.7% of total NPP (2111 kg C yr\(^{-1}\) per capita). Based on the total freshwater withdrawal of 3511 km\(^3\) yr\(^{-1}\) (FAO AquaStat), WUE of human activities (here, defined as HANPP divided by freshwater withdrawal) can be calculated as 3.67 g C kg\(^{-1}\) H\(_2\)O at the global scale. A country-based analysis revealed different aspects of the human–nature relationship in terms of WUE. The country-total NPP was strongly correlated with total precipitation (Fig. 7a), implying that carbon-related ecosystem services (e.g., provisional service for food and fiber and climate regulation service; Millennium Ecosystem Assessment 2005) are limited by water availability to a great extent. The relationship

<p>| Table 2. Observed water-use efficiencies in various biomes. |</p>
<table>
<thead>
<tr>
<th>Biome types</th>
<th>Definitions</th>
<th>WUE (g C kg(^{-1}) H(_2)O)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Evergreen broadleaf forest</td>
<td>GPP/AET</td>
<td>1.88</td>
<td>Yu et al. (2008)</td>
</tr>
<tr>
<td>Subtropical, China</td>
<td>GPP/AET (daytime)</td>
<td>0.52–3.66</td>
<td>Buermann and Schulze (1999)</td>
</tr>
<tr>
<td>Eucalyptus species, Australia</td>
<td>GPP/AET (daytime)</td>
<td>2.98–6.07</td>
<td>Beer et al. (2009)</td>
</tr>
<tr>
<td>Flux Network (FluxNet) sites (n = 4)</td>
<td>GPP/AET</td>
<td>0.95–1.0</td>
<td>Law et al. (2000)</td>
</tr>
<tr>
<td>FluxNet sites (n = 13)</td>
<td>GPP/AET</td>
<td>2.78–3.16</td>
<td></td>
</tr>
<tr>
<td>Pseudotsuga species, Canada</td>
<td>GPP/AET</td>
<td>3.1–5.3</td>
<td>Jassal et al. (2009)</td>
</tr>
<tr>
<td>Pinus species, China</td>
<td>GPP/AET</td>
<td>2.53–2.57</td>
<td>Yu et al. (2008)</td>
</tr>
<tr>
<td>Pinus species, Canada</td>
<td>GPP/TR</td>
<td>2.93–3.71</td>
<td>Brümmer et al. (2012)</td>
</tr>
<tr>
<td>Pseudotsuga species, Canada</td>
<td>GPP/TR</td>
<td>6.07</td>
<td>Brümmer et al. (2012)</td>
</tr>
<tr>
<td>Deciduous broadleaf forest</td>
<td>GPP/AET</td>
<td>2.35–5.42</td>
<td>Beer et al. (2009)</td>
</tr>
<tr>
<td>Populus species, Canada</td>
<td>GPP/AET (daytime)</td>
<td>1.83</td>
<td>Buermann and Schulze (1999)</td>
</tr>
<tr>
<td>Deciduous needleleaf forest</td>
<td>GPP/AET (daytime)</td>
<td>1.29</td>
<td>Buermann and Schulze (1999)</td>
</tr>
<tr>
<td>Larix species, Siberia</td>
<td>GPP/AET</td>
<td>2.1–4.35</td>
<td>Beer et al. (2009)</td>
</tr>
<tr>
<td>Grassland</td>
<td>GPP/AET</td>
<td>1.65</td>
<td>Buermann and Schulze (1999)</td>
</tr>
<tr>
<td>C4-dominated, United States</td>
<td>GPP/AET</td>
<td>0.41–1.26</td>
<td>Hu et al. (2008)</td>
</tr>
<tr>
<td>Steppe, China</td>
<td>GPP/AET</td>
<td>1.47</td>
<td>Li et al. (2008)</td>
</tr>
<tr>
<td>Savanna, Niger</td>
<td>GPP/AET (daytime)</td>
<td>1.51</td>
<td>Buermann and Schulze (1999)</td>
</tr>
<tr>
<td>Savanna, Australia</td>
<td>GPP/AET (daytime)</td>
<td>1.53–2.27</td>
<td>Schymanski et al. (2008)</td>
</tr>
<tr>
<td>Cropland</td>
<td>GPP/AET</td>
<td>1.57–4.02</td>
<td>Beer et al. (2009)</td>
</tr>
<tr>
<td>Wetland</td>
<td>GPP/AET</td>
<td>1.23–1.73</td>
<td>Beer et al. (2009)</td>
</tr>
<tr>
<td>Wetland sites (n = 2)</td>
<td>GPP/AET</td>
<td>1.89–3.28</td>
<td>Brümmer et al. (2012)</td>
</tr>
</tbody>
</table>
between area-based NPP and precipitation (i.e., country-size effect was removed) shows a saturation curve, supporting the relationship found from field observations and used as an empirical model to estimate NPP (Miami model; Lieth 1975). Country-total human appropriation of NPP was well correlated ($r^2 = 0.56$) with agricultural water withdrawal (Fig. 7b), implying concurrence in human activities. However, there is a wide range of scattering around the regression line, probably because of the differences in water management and form of human appropriation (e.g., agriculture and forestry). Namely, countries above the regression line would be more efficient in terms of NPP use at the cost of unit water withdrawal.

e. Limitations and advantages of the present analyses

With regard to uncertainty, the results presented here were derived using a single model, but model comparison studies revealed that a wide range of results could be obtained from different models. For example, NPP was estimated in the range of 44.4–66.3 Pg C yr$^{-1}$ by 17 models using a common dataset (Cramer et al. 1999). Using the total AET in this study ($65.0 \times 10^9$ km$^3$), total WUE$_S$ varied from 0.68 to 1.02 g C g$^{-1}$ H$_2$O when using the NPP estimates from the 17 models of Cramer et al. (1999). In the present study, the model simulations were conducted at monthly time step, which is typical as a current global-scale analysis limited by computational cost and climate data availability. However, uncertainty and potential biases caused by different time steps have not been adequately discussed. Several studies (e.g., Garcia-Quijano and Barros 2005) imply that water stresses at subdaily time scales such as midday vapor and soil water depression can reduce plant gas exchange. Because of nonlinearity in the responses of transpiration and photosynthesis, the subdaily variability may affect the estimation of gross fluxes and WUE values. To solve this problem, we should include some temporal upscaling (e.g., Daly et al. 2004) or use models with shorter time steps (e.g., 30 min: Ito et al. 2007). Moreover, the water budget scheme used in the VISIT model is simple and does not explicitly simulate groundwater dynamics and water management practices. This limitation is especially serious for irrigated croplands, where the model might underestimate AET, and perhaps for arid grasslands and deserts, where plants utilize deep water (e.g., Schenk and Jackson 2002). For example, Rost et al. (2008) estimated that agricultural use of irrigation water accounts for approximately $0.64–1.36 \times 10^{15}$ kg H$_2$O yr$^{-1}$. If this water use is added to the AET estimated in this study, the resultant WUE of croplands is decreased by 8%–16% for the present productivity. Note that irrigation can also increase productivity and then at least partly improve WUE in croplands. To overcome this limitation, the ecosystem model should be coupled with appropriate water-resource models (e.g., Döll et al.
Another limitation of this study is that the impact of nutrient limitation (nitrogen and phosphorus) on the carbon and water cycles was not assessed because we focused on climatic and land-use factors. Increased nitrogen deposition and fertilizer input could enhance terrestrial productivity and therefore WUE. Further analyses are required to evaluate this effect.

One advantage of this study, however, is that the approach adopted (i.e., analysis of WUE based on a terrestrial ecosystem model simulation) allowed us to examine carbon and water processes in a manner complementary to hydrological water-resource assessment. This approach is particularly effective for investigating biogeochemical cycling from an ecohydrological perspective, and discussing ecosystem services, in which a wide spectrum of factors such as carbon sink, water supply, biodiversity, and conservation are taken into account.

4. Conclusions

A better understanding of WUE will help to improve ecosystem management for mitigation of as well as adaptation to global environmental change. This study estimated WUE of the terrestrial biosphere as a key, integrated parameter of the water and carbon cycles under a changing environment. According to our simulations, the terrestrial biosphere would produce new plant biomass at the rate of about 0.9 g C kg\(^{-1}\) water loss by evapotranspiration (i.e., WUE\(_{3}\)). Although both
the water and carbon cycles are colimited by humidity and radiation and share aerodynamic diffusion pathways, the difference in environmental responsiveness between the two processes results in geographic heterogeneity in the estimated WUE (Fig. 4). The historical change in total WUE (Fig. 5) indicates that the terrestrial biosphere has used freshwater increasingly effectively during the past century. This finding implies that terrestrial production would be increasingly sensitive to changes in water availability (e.g., soil water), suggesting that a more reliable projection of water resources and an improved understanding of ecosystem processes related to water use are necessary. Because a water deficit is prevented by a sufficient water supply in managed croplands, mean WUE in croplands (0.85 g C kg\(^{-1}\) H\(_2\)O) is generally lower than that in natural ecosystems (0.92 g C kg\(^{-1}\) H\(_2\)O). Therefore, the past conversion of natural ecosystems into croplands may have lowered the total WUE, with considerable effects on biospheric metabolism. For example, a vast area of the world’s forests has been converted into biofuel croplands. The impacts of land-use conversion for biofuel production on the large-scale water budget remain unclear (e.g., Mulder et al. 2010), and investigating these impacts is an urgent task. Our analyses imply that land use can lead to a decline in WUE. This finding is important for evaluating total ecosystem services not only with regard to the greenhouse gas budget but also the water-resource supply.

Acknowledgments. This study was supported in part by a Grant-in-Aid for Scientific Research (Grants 19310017 and 21114010) from the Japan Society for the Promotion of Science and the Ministry of Education, Culture, Sports, Science, and Technology.

REFERENCES


Bert, D., S. W. Leavitt, and J.-L. Dupouey, 1997: Variations of wood \(\delta^{13}C\) and water-use efficiency of \(\text{Abies alba}\) during the last century. Ecology, 78, 1588–1596.


——, and Coauthors, 2001: Global response of terrestrial ecosystem structure and function to CO\(_2\) and climate change: Results


Law, B. E., R. H. Waring, P. M. Anthone, and J. D. Aber, 2000: Measurements of gross and net ecosystem productivity and water vapour exchange of a Pinus ponderosa ecosystem, and...
Schulze, E.-D., R. H. Robichaux, J. Grace, P. W. Rundel, and J. R. Ehleringer, 1987: Plant water balance: In diverse habitats, where water often is scarce, plants display a variety of mechanisms for managing this essential resource. Bioscience, 37, 30–37.