Gross primary production, ecosystem respiration and net ecosystem exchange in Asian rice paddy: an eddy covariance-based approach

P. Bhattacharyya*, S. Neogi, K. S. Roy and K. S. Rao
Division of Crop Production, Central Rice Research Institute, Cuttack 753 006, India

Carbon dioxide (CO₂) exchange between the terrestrial ecosystems and the atmosphere is one of the major processes affecting atmospheric CO₂ concentration. In various ecosystems in the world long-term observations of CO₂ exchange have been made for assessing the role of terrestrial ecosystems in the present-day global CO₂ budget and to predict its changes in the future climatic scenario. The eddy covariance (EC) system can provide a measure of net ecosystem exchange (NEE), which can be partitioned into gross primary production (GPP) and ecosystem respiration (RE) using mathematical modelling approach helpful for characterization of ecosystem carbon budgets. The EC technique for measuring CO₂, water vapour and energy fluxes between the biosphere and the atmosphere is widely used in various regional networks. Presently, more than 400 EC sites are operational worldwide measuring carbon exchange in different biomes and climatic conditions at high temporal resolution. Rice paddy fields are widespread in monsoon Asia and the carbon exchange between paddy fields and the atmosphere is greatly influenced by cultivation and field management practices. In this review, an attempt has been made to summarize NEE, GPP and RE with the help of EC system in Asian rice paddies focusing on CO₂ exchange between the biosphere and the atmosphere.

Keywords: Ecosystem respiration, eddy covariance, gross primary production, net ecosystem exchange, rice paddy.

GLOBAL budgeting of the greenhouse gas (GHG) exchanges between ecosystems (terrestrial, aquatic) and the atmosphere is one of the key issues of climate change research. There is a need to monitor and quantify GHG exchanges in the various ecosystems prevalent in the world. There has been a drastic increase in the atmospheric concentration of GHGs, viz. carbon dioxide (CO₂), methane (CH₄), nitrous oxide (N₂O), etc. since the industrial revolution because of fossil-fuel combustion, land-use change, deforestation and intensification of agriculture. Agriculture accounted for an estimated emission of 5.1 to 6.1 GtCO₂-eq yr⁻¹ GHGs in 2005 (10–12% of total global anthropogenic emissions of GHGs)¹. Global atmospheric concentration of CO₂ has increased markedly as a result of human activities since 1750 (pre-industrial era) from 280 to 379 ppmv in 2005 and is currently increasing at the rate of 1.9 ppmv yr⁻¹. Despite large annual exchanges of CO₂ between the atmosphere and agricultural lands, the net flux is approximately balanced, with CO₂ emissions only around 0.04 Gt CO₂ yr⁻¹. Agriculture releases to the atmosphere a significant amount of CO₂ along with CH₄ and N₂O. Carbon dioxide is released largely from microbial decay or burning of plant litter and soil organic matter³.⁴. According to the US-EPA estimation, net CO₂ emission from the soil is less than 1% of global anthropogenic CO₂ emissions. Half of the anthropogenically released CO₂ may be absorbed in the terrestrial biosphere, the soil or the ocean, or some combination of all three¹. Agro-ecosystems are equally important and contribute to regional carbon budget where crops are dominant⁶ and, therefore, proper methodology is required for the upscaling and budgeting of carbon exchange components in crop lands. Carbon dioxide flux measurements of agro-ecosystems in relation to photosynthesis and respiration over crops and their response to environmental variables are vital for understanding the physiological behaviour of agro-ecosystems and predicting future climate change⁶.

Rice is the major crop in Asia and the area of rice paddies in this region is about 87% of the world’s total rice cultivated area⁷ and about 80% of it is grown under flooded conditions⁸. Rice is grown in different environments, in varied climatic (tropical to temperate), edaphic and biological conditions and different agricultural management practices (viz. ploughing, manure amendment, seeding, transplanting, water management, harvest), which affect the rates of CO₂ and CH₄ emissions⁹. Therefore, it is important to quantify CO₂ exchange in paddy fields in Asia, where the highest number of such fields in the world exists. The eddy covariance (EC) technique has been widely employed for CO₂, water vapour and heat
The net ecosystem exchange (NEE) of CO₂ between the biosphere and the atmosphere is the balance between the fluxes associated with photosynthetic assimilation by the foliage (gross primary production, GPP) and respiratory effluxes (RE) from autotrophs and heterotrophs (microbial and soil fauna)¹⁸.

\[
\text{NEE} = \text{RE} - \text{GPP} \quad \text{(ref. 19).}
\]

**Eddy covariance system for CO₂ flux measurement**

The EC technique is widely employed as the standard micrometeorological method to monitor fluxes of CO₂, water vapour and heat, which are necessary to determine CO₂ and heat balances of land surfaces²⁵. The EC technique has become the most important method for measuring trace gas exchange between terrestrial ecosystems and the atmosphere²²,²⁶. It can represent a large area of land at the ecosystem scale than the typical plot area²⁷–⁳¹ for a short period or even for several years. It has become the backbone for bottom-up estimates of continental carbon balance from hourly to inter-annual timescales²²,³²–³⁵. The EC technique is based on high frequency (10–20 Hz) measurements of wind speed and direction as well as CO₂ and H₂O concentrations at a point over the canopy using a three-axis sonic anemometer and a fast-response infrared gas analyser²⁵,³⁶,³⁷ (Figure 2). The two sensors, three-
Figure 2. Eddy covariance system for CO\textsubscript{2} flux measurement installed in the rice field of CRRI, Cuttack.

Axis sonic anemometer and fast-response infrared gas analyzer, are normally installed at 2–3 m height (depending on the rice crop canopy height) on a tripod mast with a sensor separation of 15–20 cm. Data obtained from the three-axis sonic anemometer and CO\textsubscript{2}/H\textsubscript{2}O infrared gas analyzer, are sampled at 10 and/or 20 Hz using a fast-response datalogger\textsuperscript{18,38,39}. The mean vertical flux density of CO\textsubscript{2} is obtained as the 30 min covariance between vertical fluctuations ($\omega'$) and CO\textsubscript{2} mixing ratio ($c'$)\textsuperscript{26}.

$$F_z = \rho_a \cdot \omega'c'.$$

In eq. (1), $\rho_a$ represents air density, the overbars denote time-averaging and primes represent fluctuations about average value. A positive covariance between $\omega'$ and $c'$ indicates net CO\textsubscript{2} transfer into the atmosphere and a negative value indicates net CO\textsubscript{2} absorption by the vegetation. NEE is calculated as the sum of CO\textsubscript{2} storage change ($F_s$) within the air space below flux measuring height and the eddy CO\textsubscript{2} flux ($F_z$).

Night-time RE (RE(N)) is determined using the EC system from night-time NEE, as at night-time NEE is equal to night-time ecosystem respiration (RE(N)), since $GPP = 0$. NEE in night-time hours is expressed as an exponential function of air temperature ($T$) and the relationship is then applied to the daytime for estimating RE in daytime (RE(D)).

$$RE(N) = R_0 Q_{10}^{(T - T_0)/10},$$

where $R_0$ and $Q_{10}$ are empirical constants determined by running regression analysis between RE(N) and temperature ($T - T_0$)/10; $T$ can either be air or soil temperature\textsuperscript{41} and $T_0$ is the reference temperature. Based on the assumption that the daytime temperature response of RE is the same as that of the RE(N), eq. (2) is applied to the daytime data to estimate daytime half-hourly RE (RE(D)) and GPP ($F_{GPP}$) is calculated as

$$F_{GPP} = -F_{NEE} + RE(D),$$

where $F_{NEE}$ denotes NEE\textsuperscript{32,43}. GPP is generally expressed as a rectangular hyperbolic function of incident photosynthetically active radiation ($Q_p$),

$$F_{GPP} = P_{max} \alpha Q_p/(P_{max} + \alpha Q_p),$$

where $P_{max}$ and $\alpha$ are empirical constants to be determined by regression between GPP and PAR. $P_{max}$ represents the hypothetical maximum of GPP or the closeness to the linear response coefficient\textsuperscript{44} and $\alpha$ denotes the initial slope of the function or ecosystem quantum yield.

There is a need to gap-fill those missing values of eddy flux data (in order to estimate seasonal NEE) which are rejected by quality control tests or due to instrument malfunctioning. For CO\textsubscript{2} flux nonlinear regression analysis is performed for gap-filling missing data of few hours or more and missing values are estimated from meteorological variables. For gap-filling of night-time NEE data, eq. (2) is used. To gap-fill daytime NEE data, RE(D) and GPP are first gap-filled. RE (D) is gap-filled using eq. (2) and GPP is gap-filled using eq. (4).

**Quantification of NEE, GPP and RE employing EC technique in Asian rice paddies**

Carbon dioxide fluxes from different Asian rice paddy ecologies at different spatio-temporal scales revealed that NEE, GPP and RE differ in different regions depending on the cropping pattern, duration, sequence of crop cycle, irrigation, drainage pattern, soil type, tillage practices and...
<table>
<thead>
<tr>
<th>Location</th>
<th>Temperature (°C)</th>
<th>Rainfall (mm)</th>
<th>Soil type</th>
<th>Fertilization</th>
<th>Drainage status</th>
<th>NEE*</th>
<th>Cropping pattern</th>
<th>Period of observation</th>
<th>Stage of crop</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bangladesh Agricultural University (BAU), Bangladesh (24.75°N lat., 90.5°E long, and 18 m amsl)</td>
<td>–</td>
<td>2175</td>
<td>Sandy loam texture</td>
<td>–</td>
<td>Irrigated</td>
<td>Integrates NEE approximately −105 g C m⁻²</td>
<td>Rice–fallow–rice</td>
<td>From 76 to 79 days after transplanting in Boro (dry season) rice–growing season 2006</td>
<td>Full heading stage of rice</td>
</tr>
<tr>
<td>BAU (24.73°N lat., 90.42°E long, and 18 m amsl)</td>
<td>25.4</td>
<td>2065</td>
<td>Sandy loam texture</td>
<td>Chemical</td>
<td>Irrigated and rinsed</td>
<td>Summer follow +22 g C m⁻², Winter follow +40 g C m⁻², Boro season NEE −290 g C m⁻², Aman season −290 g C m⁻², Whole year NEE −527 g C m⁻²</td>
<td>Rice–fallow–rice</td>
<td>Whole year of 2007, including two cropping seasons and two fallow periods</td>
<td>Vegetative to harvesting period of two crop-growing seasons plus fallow periods</td>
</tr>
<tr>
<td>International Rice Research Institute (IRRI), The Philippines (14°09'53&quot;N, 120°15'14&quot;E, 21 m amsl)</td>
<td>27</td>
<td>1971</td>
<td>Silty clay loam</td>
<td>Chemical</td>
<td>Irrigated</td>
<td>Flooded rice fields integrated season-long NEE is −258 g C m⁻², whereas in aerobic rice fields integrated season-long NEE is −85 g C m⁻²</td>
<td>Rice–rice</td>
<td>From 60 to 118 days after transplanting (flooded rice) and/or days after sowing (aerobic rice), dry season 2008</td>
<td>Vegetative to harvesting stage</td>
</tr>
<tr>
<td>Taiwan (23°58'13.5&quot;N lat., and 120°39'27.2&quot;E long, having an elevation of 100 m amsl)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Chemical</td>
<td>Drained</td>
<td>Integrates NEE approximately +22.1 g C m⁻² for one month</td>
<td>Rice–rice</td>
<td>One month, 24 October – 23 November 2006 (2 cropping season)</td>
<td>Heading to maturity stage of the crop</td>
</tr>
<tr>
<td>Mase paddies flux site, Japan (36°03'N lat., 140°01'E long, and 15 m amsl)</td>
<td>13.5</td>
<td>1255.6</td>
<td>Clay loam</td>
<td>Chemical</td>
<td>Irrigated</td>
<td>Integrates NEE approximately −397.64 g C m⁻²</td>
<td>Rice</td>
<td>Primary crop period, from 2 May–18 September 2002</td>
<td>Transplanting to harvesting</td>
</tr>
<tr>
<td>Okayama University, Japan (34°32'N lat., 133°36'E long, and 2 m amsl)</td>
<td>–</td>
<td>–</td>
<td>Clay</td>
<td>Chemical</td>
<td>Irrigated and drained</td>
<td>Integrates NEE approximately −47.62 g C m⁻²</td>
<td>Rice–rice</td>
<td>Almost see week, 6–13 August 1996</td>
<td>A month before heading stage of crop</td>
</tr>
<tr>
<td>Central Rice Research Institute, India (20°27.113°N lat., 85°56.416°E long, and 24 m amsl)</td>
<td>27.7</td>
<td>1500</td>
<td>Clay loam</td>
<td>Chemical</td>
<td>Irrigated</td>
<td>Integrates NEE: −314 g C m⁻², rabi (dry) season, 2010–11 (unpublished data)</td>
<td>Rice–fallow–rice</td>
<td>Ten days after transplanting to maturity during rabi (dry) season, 2010–11</td>
<td>Vegetative to maturity stage</td>
</tr>
<tr>
<td>China (28°55'N lat., 111°27'E long.)</td>
<td>16.5</td>
<td>1448</td>
<td>Red clay</td>
<td>–</td>
<td>–</td>
<td>Annual cumulative total soil respiration is about 425.45, 616.36 and 621.82 g C m⁻²</td>
<td>Rice–rice–fallow</td>
<td>Annual observations of soil respiration of the years 2003, 2004 and 2005 respectively</td>
<td>Total rice-growing seasons along with fallow periods</td>
</tr>
</tbody>
</table>

*Negative NEE represents CO₂ fluxes from atmosphere towards the rice field (CO₂ absorption or uptake by rice), whereas positive NEE represents CO₂ fluxes from rice fields towards the atmosphere (CO₂ emission from the rice field).
climate parameters (Table 1). The CO2 fluxes quantified by the EC technique were used to study the inter-relationship of NEE in some selected Asian rice paddies. At an agricultural farm in Bangladesh, rice paddies exhibited a clear diurnal pattern in CO2 fluxes. NEE ranged from –38 to 10 μmol CO2 m–2 s–1 during heading stage (70–79 DAT) in boro rice (dry season rice), 2006. It showed a daytime uptake (negative NEE, i.e. uptake of CO2 due to photosynthetic assimilation) and night-time release of CO2 (positive NEE, i.e. emission of CO2 due to respiration in the absence of photosynthesis) from the canopy leading to net cumulative NEE of –105 g C m–2 (Table 1).

Season-long measurement of CO2 flux employing the EC method to study the CO2 budget in single rice-cropping paddy field was made at the Mase paddy flux site, in central Japan (13) (Table 1). During the mid-vegetative stage the paddy field became the net CO2 sink and diurnal variation of NEE became prominent. NEE reached its peak in heading stage with the midday uptake of –29.55 μmol CO2 m–2 s–1 and night-time release of +6.82 μmol CO2 m–2 s–1 (Figure 3 a).

In the International Rice Research Institute (IRRI), the Philippines during dry season 2008, NEE was monitored in both flooded and aerobic rice fields (16). NEE was about –10 μmol CO2 m–2 s–1 from active tillering to panicle initiation stage, and it reached a lowest value of –22 μmol CO2 m–2 s–1 (Figure 3 b) during heading to flowering stage in flooded rice fields. From tillering to ripening stage, the flooded rice fields behaved as net CO2 sink on daily basis. On the other hand, aerobic rice fields behaved as net CO2 sink from reproductive to harvesting stage with the mean value of –2.23 μmol CO2 m–2 s–1.

In central Taiwan (Table 1), CO2 fluxes showed a clear diurnal pattern during rice maturity period (from 24 October to 23 November 2006) (9). The fluxes and concentration of CO2 were measured by the EC system mounted at 27.5 m above ground level. During the study period the daily values of CO2 exchange ranged from –17.03 to 27.5 μmol CO2 m–2 s–1 having a standard deviation of 4.7 μmol m–2 s–1. But the diurnal mean hourly composite of CO2 flux ranged between –7 and +7 μmol CO2 m–2 s–1 (Figure 3 c). As a whole, during the measurement period, the rice paddy ecosystem behaved as a potential CO2 source with a daily average flux of 0.71 μmol CO2 m–2 s–1 and contributed to atmosphere 22.1 g C m–2 (Table 1).

In the experimental farm of CRRRI, diurnal variations in mean NEE during the rabi (dry) season of 2010–11 were monitored with the help of the EC system, and the values of NEE varied between +3.87 and –19.22 μmol CO2 m–2 s–1 depending upon the crop phenology (Figure 3 d). Maximum NEE and GPP by rice crop was found between 12.00 and 14.00 h, whereas maximum RE was found between 12.00 and 15.00 h over the cropping season (Figure 3 d). The average daily CO2 concentration in the atmosphere varied between 360 and 385 μmol mol–1 during the entire course of study (Figure 4). Plant photosynthesis during the daytime led to the uptake of CO2 from the atmosphere whereas respiration at night contributed to an efflux of CO2 to the atmosphere in the absence of photosynthesis. Rice crop behaved as a net CO2 emitter.

In Bangladesh, one year continuous monitoring of CO2 fluxes was done by a tower-based EC system in a double-cropping paddy field (Table 1) for evaluating seasonal variation of RE (15). Boro rice is cultivated in the dry season, from late winter (February) to mid-summer (May), under irrigated condition, whereas aman rice (wet-season rice) is cultivated mostly in the rainy season, from August to early winter (December) in rainfed condition. The seasonal variation in daily RE in the rice field was characterized by two annual peaks (Figure 5 a), one in the late-boro season (mid-May) and another in the mid-aman season (late September). The peak in the boro season was larger. During the summer fallow period considerable large RE was observed, which was caused by respiration of the ratoon crop. RE during the summer fallow period was almost balanced by active photosynthetically CO2 assimilation with a resultant NEE of 22 g C m–2 (Figure 5 b). The integrated cumulative RE values for the boro season, summer fallow period, aman season, winter fallow period and for total annual scale were 412, 257, 311, 68 and 1047 g C m–2 respectively. The integrated GPP and NEE values were in the order of 711, 235, 601, 28 and 1574 g C m–2 and –299, 22, –290, 40 and –527 g C m–2 respectively, for boro season, summer fallow period, aman season, winter fallow period and for total annual scale in 2007 (Figure 5 b).

The total C budget integrated over the rice cropping period showed that the NEE in flooded rice fields (–258 g C m–2) was about three times higher than that of aerobic rice fields (–85 g C m–2 in IRRI) (16) (Table 1; Figure 5 e). The integrated seasonal GPP and RE values for flooded and aerobic rice fields were 778 and 521 g C m–2, and 515 and 430 g C m–2 respectively (Figure 5 e).

In the Mase paddy flux site in central Japan, the rice plant biomass over the season exhibited seasonal changes which affected ecosystem respiration (19). The mid-season and pre-harvest drainages also affected ecosystem respiration because removal of standing water enhanced direct CO2 diffusion from the soil. It was found that the ecosystem respiration in the late growing period was dominated by rice plant respiration as a result of large above-ground biomass. In a nutshell, the daily net ecosystem CO2 exchange showed a seasonal variation and the maximum uptake rate in a day was –10.64 g C m–2 when the leaf area index of rice reached its peak. On a seasonal scale the integrated GPP, RE and NEE values of the primary crop period were 1143.55, 745.91 and –397.64 g C m–2 respectively (Figure 5 d).
Figure 3. Diurnal variations in half-hourly NEE in a rice growing season in (a) Japan in heading stage of rice (24–31 July 2002), (b) in heading to flowering stage of rice (12 March–1 April 2008) in International Rice Research Institute, the Philippines, (c) in heading to maturity stage of rice in Taiwan (24 October–23 November 2006) and (d) in CRRI, Cuttack along with the diurnal variations in half-hourly GPP and RE observed during rabi (dry) season of 2010–11 from transplanting to harvesting stage (31 January–10 May 2011).

Figure 4. Diurnal changes in mean CO₂ concentration observed during the rabi season 2010–11 at CRRI, Cuttack.

The measurement of CO₂ fluxes over the rice canopy was made for eight days, about a month before heading of the rice plants at the experimental farm of Okayama University, Japan⁸ (Table 1). It was noticed that the daily net uptake of CO₂ from the atmosphere by the paddy field was 50% lower when the paddy was drained than when it was flooded. Enhanced fluxes of CO₂ from the drained soil due to removal of flood water acted as a barrier to gas transport from soil to air. The average CO₂ flux (NEE) during drained and flooded conditions was –3.81 and –7.63 μmol CO₂ m⁻² s⁻¹ respectively, and the total integrated NEE over those eight days was estimated to be –47.62 g C m⁻² (Table 1).

The annual and seasonal variation of soil respiration was also noticed in rice field of China¹². The total cumulative annual soil respiration of paddy soil in the subtropical region of China was 425.45, 616.36 and 621.82 g C m⁻² in 2003, 2004 and 2005 respectively (Figure 5 e).

In CRRI, the seasonal cumulative NEE, GPP and RE were –341, 636 and 295 g C m⁻² respectively, in lowland rice field (Table 1; Figure 5 f). It is evident from the findings that the lowland rice fields sequestered carbon from the atmosphere, which is attributed to higher photosynthetic capacity of lowland rice to convert atmospheric carbon into organic compounds and to slow down organic matter decomposition in flooded soils. Similar results were reported from Taiwan, Japan, the Philippines and Bangladesh under lowland rice field⁹,¹³,¹⁴,¹⁶.
Important factors affecting NEE

Factors controlling gas exchange between rice paddies and the atmosphere are of varying nature because they are cultivated under submerged condition. Flooding and drainage affect CO2 exchange in paddy fields8. The changes of micrometeorological environment with flooding influence root activity, photosynthesis and respiration of rice plants. The activity of aquatic plants such as algae in the floodwater may also affect CO2 exchange between rice paddies and the atmosphere8. The characteristics of CO2 exchange over rice canopy have a relationship with several ecosystem parameters and environmental variables (latent heat, air temperature, vapour pressure deficit, canopy irradiance, heat stress, stomatal response, high evaporative demand, circadian rhythm, growth stages of rice crop, leaf area index, biomass, etc.6,45. The amplitude of the diurnal variation in NEE increases as leaf area index at different crop growth stages advances and reaches its peak around the anthesis/heading to flowering stage6. The diurnal pattern of CO2 flux and carbon uptake is dependent on sunlight. This is due to leaf gas exchange and pattern of light interception by the canopy45–47. The CO2 flux pattern is also dependent on physical environmental conditions and is particularly sensitive to climate change.
Summary and discussion

NEE between rice paddies and the atmosphere is controlled by several biological and physical processes. During the daytime, plant photosynthesis leads to the uptake of CO₂ from the atmosphere and respiration at night leads to an efflux of CO₂ to the atmosphere in the absence of photosynthesis. During the harvesting or maturity stage when the rice fields remain drained, the rice paddies along with the soil system behave as a net CO₂ source, but most of the times during the crop season rice paddies act as CO₂ sink. The carbon dynamics in terrestrial vegetation follows complex pathways and shows variability at different timescales starting from diurnal, seasonal, annual and inter-annual. The EC technique and measures directly the net ecosystem CO₂ exchange, which is a powerful micrometeorological technique for characterization of carbon budget in terrestrial ecosystems. This method can account for all the components of carbon fluxes required for accurate quantification of carbon exchange at the landscape level with regard to a particular vegetation.

Further studies are required to continuously monitor and estimate diurnal, seasonal, annual, inter-annual and even long-term variations in CO₂ exchange and carbon budget, including the fallow periods in different rice-production systems under different agro-climatic zones. Moreover, the studies should focus on how they are affected by microclimate and or climatic variables and land-surface characteristics prevalent in each location in double-cropping rice paddy fields in monsoonal South and Southeast Asian countries, where rice is grown as a staple food. As many of the factors controlling gas exchange between rice paddies and the atmosphere are different from other ecosystems, field studies should be designed to measure net fluxes and to improve understanding of the factors, including detailed mechanisms controlling the fluxes. Moreover, accurate quantification of carbon exchange in the tropical flooded rice paddy ecosystem is extremely important to determine carbon stock in that ecosystem. EC studies for CO₂, water vapour and energy fluxes in the ecosystem if coupled with other important components may be employed to estimate net ecosystem production or for assessing net ecosystem carbon budget. EC measurements using tunable diode laser absorption spectroscopy and quantum cascade laser absorption spectroscopy are now becoming available among the FLUXNET communities worldwide for improved trace gas (NH₃, NOₓ, NO₂, CH₂ and CO₂) analysis. This tool could be helpful for monitoring and estimation of GHGs and their budgeting via ecosystem modelling approach. These high-resolution process-based models can be applied to upscale and validate GHG emissions from any point-scale cropland to local, regional, national level to help in predicting future anticipated climate changes.


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