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High sensitivity of a tropical rainforest to water variability: Evidence from 10 years of inventory and eddy flux data

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[1] The response of tropical rainforest to environmental perturbation is of critical importance given their potential to mitigate climate change. Nevertheless, it was not well addressed to date. Therefore, related hypotheses, i.e., CO_2 fertilization–related accelerating growth hypothesis (AGH) and remote sensing–based drought resilience hypothesis (DRH), were necessarily to be testified. Here these hypotheses were tested through 10 years of annual inventory records and half-hourly eddy flux measurements from a tropical rainforest. We show that the studied forest is highly sensitive to water variability, with low canopy photosynthesis, slow stand growth, and high mortality rate in dry years, especially in the severe drought. Ecosystem respiration was not correlated with net water balance within years, but significant correlations were found between these parameters with a time lag of 10–15 months. A boom of photosynthesis in 1 year post drought was most probably a result of nutrient pulse–related drought. In general, neither AGH nor DRH was supported by the study. Given predictions that tropical areas will experience increasingly dry conditions in the future, much attention should be paid to the potential fate of carbon sink in tropical rainforests.

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1. Introduction

[2] Growth trends in, and drought sensitivity of, tropical forests have been subjects of study for decades. Tropical forests have been reported to be growing faster over the past two or three decades as a result of "CO_2 fertilization" [*Laurance et al.*, 2004; *Lewis et al.*, 2004]. The so called "accelerating growth of tropical forests" hypothesis (AGH), however, is debatable in part because only one method—a multiple-year census interval and a short series of recensusing—was used [*Clark and Clark*, 2011]. Moreover, no direct evidence of CO_2 fertilization of tropical forests has been provided to date [*Huntingford*, 2013; *Clark et al.*, 2013].

[3] The drought sensitivity of tropical forests is more controversial, and two contrasting perspectives exist, i.e., tropical forests are either resilient or sensitive to drought. A study based on the National Aeronautics and Space Administration (NASA) satellite images showed an Amazonian rainforest "green-up" during the severe drought of 2005 [*Saleska et al.*, 2007]. This phenomenon suggested that tropical forests could be resilient to drought (the drought resilience hypothesis, DRH). The resilience of this forest was attributed to the existence of deep roots that were able to access water available far down in the soil profile [*Nepstad et al.*, 1994]. Inventory data, on the other hand, provided evidence that the Amazonian rainforest was sensitive to drought; both decreased growth and increased mortality were observed in the forest during the 2005 drought [*Phillips et al.*, 2009]. Manipulative, rainfall-exclusion experiments also provided support to the position that tropical rainforests are sensitive to drought [*da Costa et al.*, 2010].

[4] The importance of resolving these contrasting perspectives is urgent. Tropical rainforests harbor a great diversity of species and play a significant role in the global carbon cycle due to their huge biomass and high productivity [*Dixon et al.*, 1994]. In this paper, we introduce 10 years of annual recensus inventory data collected in a tropical rainforest to examine the AGH and the DRH. Since both enhanced photosynthesis and aboveground carbon allocation could contribute to increased tree growth, 10 year eddy flux data were compiled as an independent approach to discern the relative contributions of these parameters. Interestingly, a severe,

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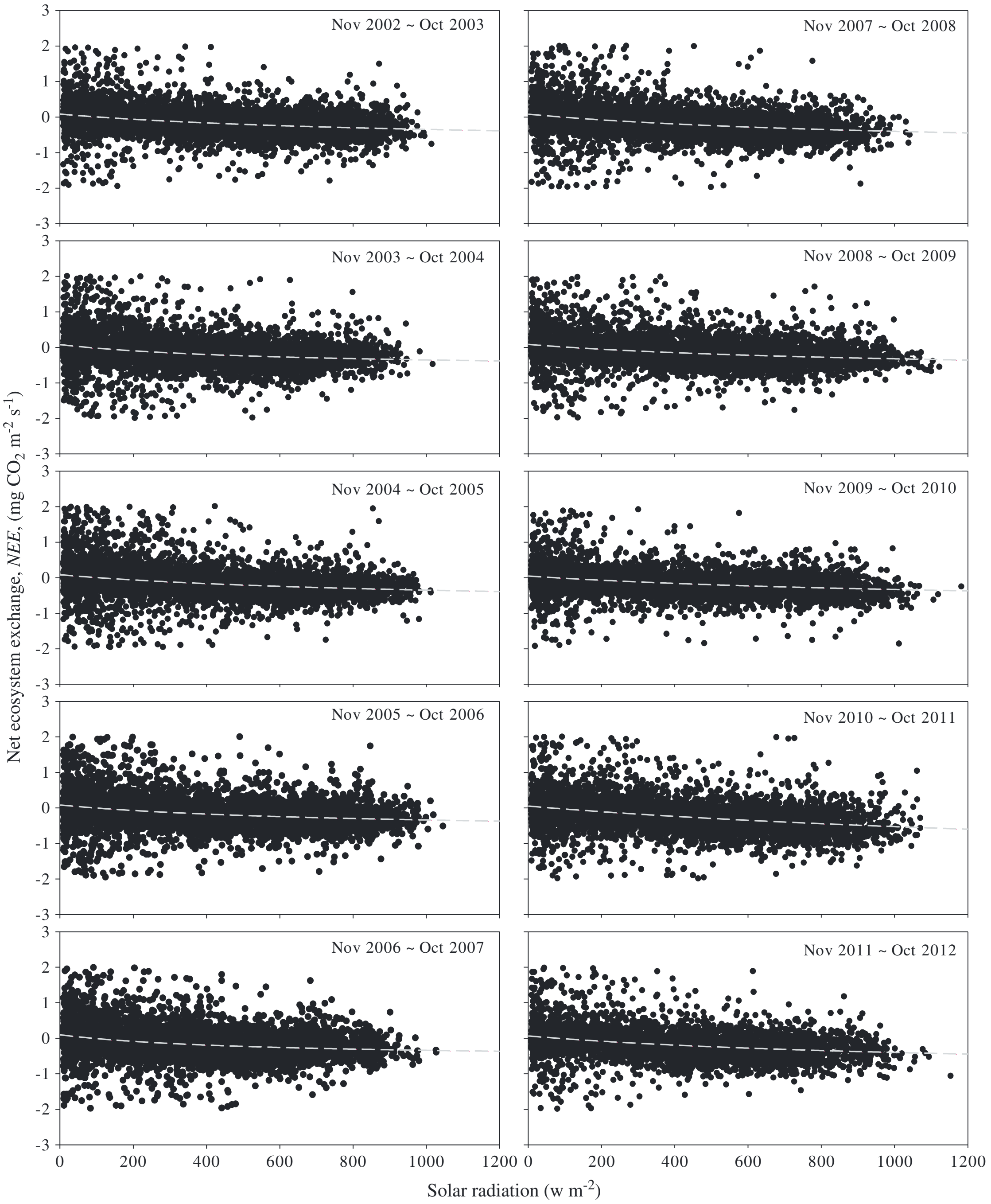

Figure 1. The light response of net ecosystem carbon exchange (NEE) according to a half-hourly data set in Xishuangbanna rainforest, China. The response was binned by hydrological year (November through the following October). The gray dashed line was fitted by the Michaelis-Menten equation.

once-a-century drought occurred in our study site, providing an opportunity to examine the seldom-addressed drought recovery issue. We also report a 10 year interannual variation in ecosystem respiration and its environmental controls.

2. Methods

2.1. Study Site

[5] The study was carried out in the National Nature Reserve of Xishuangbanna, China (21°55′39″N, 101°15′55″E, 750 m above sea level). The climate is strongly seasonal in this area and dominated by the South Asian monsoon. Thirteen percent of annual rainfall occurs from November through April, the period defined as the dry season. Mean annual temperature and rainfall are 21°C and 1492 mm, respectively. The primary vegetation in the area is tropical rainforest with a canopy height of approximately 35 m. Species richness is high and similar to that of other rainforests [*Cao et al.*, 2006]. The presence of large logs, many epiphytes, an uneven age distribution, and complex canopy characterizes the forest as “old growth” [*Tan et al.*, 2010]. A permanent, 1 ha ecological research plot is located in the center of the

Table 1. The Canopy Photosynthesis Light Response Parameters[a]

Period	α (μg CO_2 per J energy)	P_{max} (mg CO_2 m^{-2} s^{-1})	R_d (mg CO_2 m^{-2} s^{-1})
2002.11–2003.10	0.837	0.805	0.086
2003.11–2004.10	0.696	0.681	0.080
2004.11–2005.10	0.875	0.859	0.084
2005.11–2006.10	0.968	0.737	0.079
2006.11–2007.10	0.649	0.657	0.094
2007.11–2008.10	0.952	0.979	0.082
2008.11–2009.10	0.820	0.800	0.086
2009.11–2010.10	0.686	0.848	0.049
2010.11–2011.10	0.866	1.728	0.048
2011.11–2012.10	0.867	0.994	0.062

[a] The Michaelis-Menten equation was used in regression.

Nature Reserve and shows no signs of recent anthropogenic disturbance. The eddy flux tower is located close to the permanent plot and covers the entire plot in its footprint. The soil is lateritic, derived from siliceous rocks such as granite and gneiss, with a pH from 4.5 to 5.5.

2.2. Inventory

[6] The 1 ha permanent plot was established in 1994 [*Cao and Zhang*, 1997], at which time all trees with diameter breast height (DBH) >2 cm were identified to the species level, tagged, and mapped. A tree inventory has been carried out annually since 1995. However, as of 2010, the census interval has been changed from 1 to 5 years due to financial constraints. In that year, the standard of inventory has also been redefined, and the data in that year were not included. In addition, there are some human-caused uncertainties in the inventory of 2005 (C. Min, personal communication, 2005). Though 11 continuous years of pre-2010 data were collected to derive 10 periods of growth and mortality, in actuality, only 7 DBH increment data were obtained, while the increment data in years 2005, 2006, and 2010 were discarded.

[7] The mean relative growth rate (RGR) was calculated as

$$\mathrm{RGR} = \mathrm{mean}\left(\frac{\mathrm{DBH}_{i+1} - \mathrm{DBH}_i}{\mathrm{DBH}_i}\right)$$

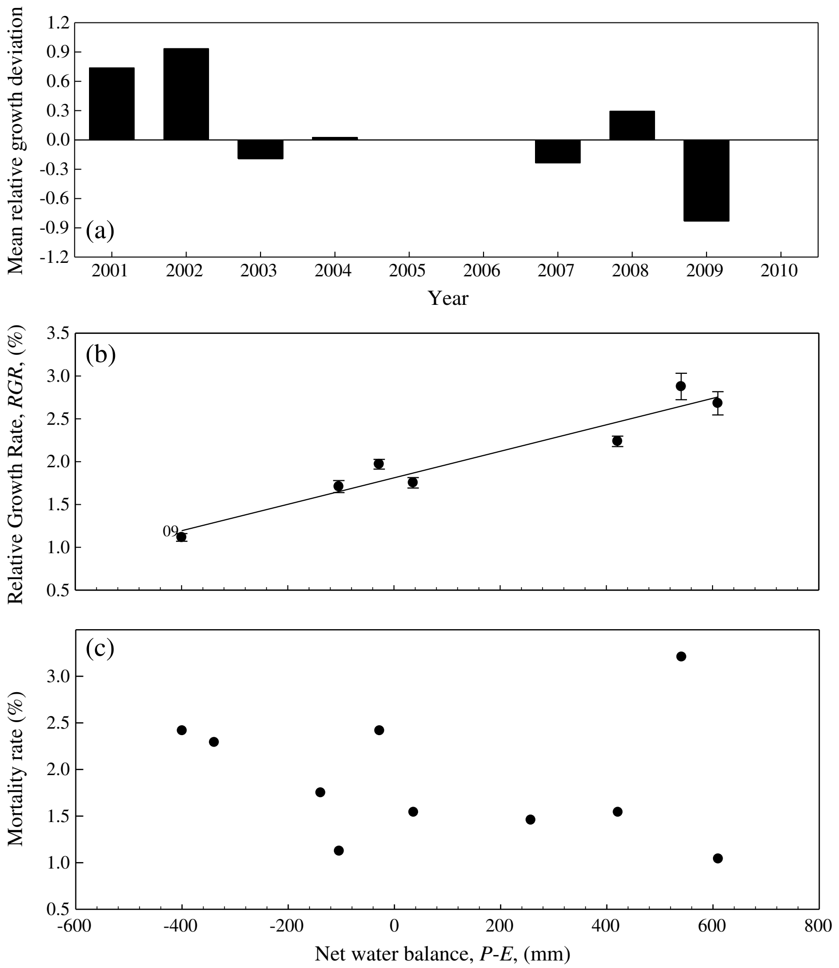

Figure 2. (a) The growth trend of Xishuangbanna tropical rainforest in the past 10 years with 7 years effective data. (b) Close positive relationship (linear regression shown by the solid line) between relative growth rate and net water balance. (c) Annual mortality rate related to net water balance. Error bars in Figure 2b represent standard errors.

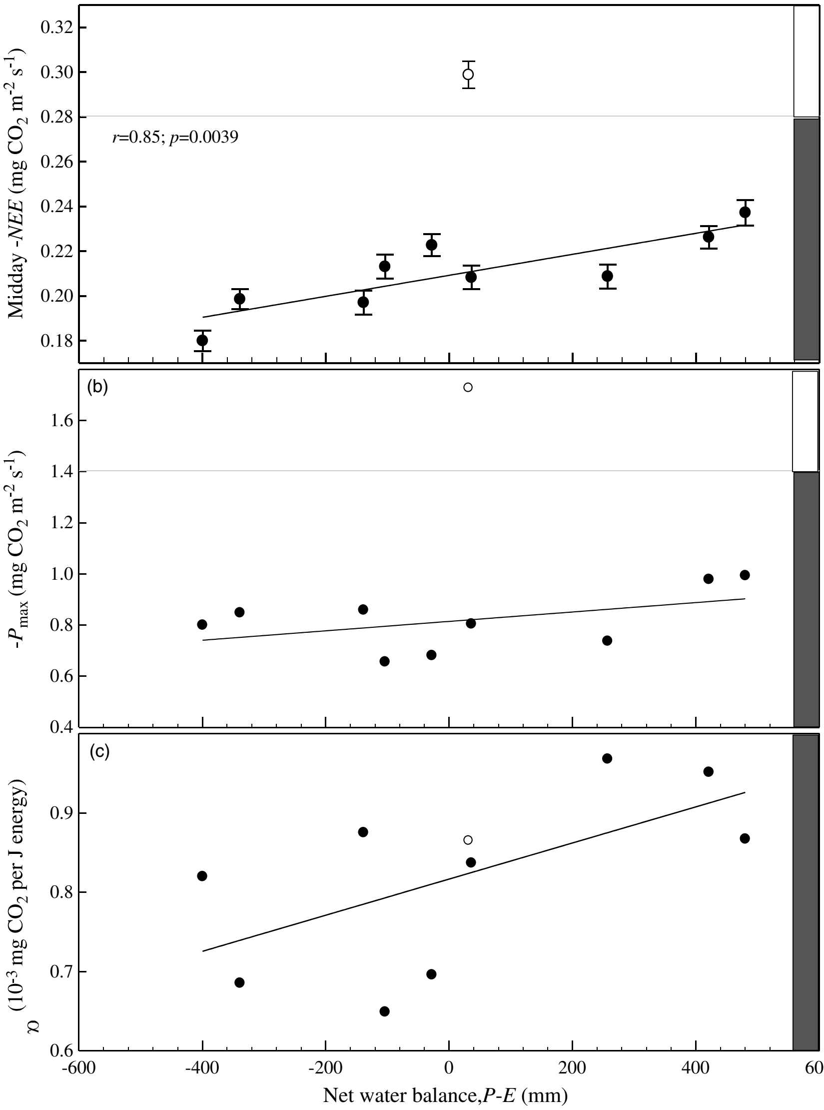

Figure 3. Relationships between (a) minus midday net ecosystem photosynthesis (−NEE), (b) minus light-saturated rate of net ecosystem photosynthesis ($-P_{\max}$), and (c) apparent quantum yield (α) and net water balance. The open circle represents the year 2011 and was not included in the regression. Error bars represent standard errors.

where DBH_i and DBH_{i+1} represent diameter at breast heights (DBHs) at year i and the following year, respectively, and i is an integer. Relative growth is commonly calculated using a logarithmic equation, i.e., ($\mathrm{RGR} = \ln(\mathrm{DBH}_{i+1}) - \ln(\mathrm{DBH}_i)$). We found a strong correlation between our calculated RGR and that calculated by the logarithmic method ($r = 0.99$, $p < 0.0001$, $n = 10$). Thus, both calculation methods were considered effective, and the results and analysis should not differ due to the calculation method used. We calculated the annual rate of tree mortality as $r = 1 - (N_t/N_0)$, as suggested by *Sheil and May* [1996], where N_0 is the number of trees recorded in the initial inventory, and N_t is the number of trees alive at the end of 1 year.

2.3. Eddy Flux

[8] In September 2002, the eddy flux system was established with the support of ChinaFLUX to represent a typical site in tropical rainforest. This location is among the first four forested eddy flux sites in China. The eddy-covariance system was mounted at a height of 48.8 m on a 70 m iron tower. The system included a three-dimensional sonic anemometer (model CSAT-3; Campbell Scientific, Inc., Logan, UT, USA) and an open-path infrared gas analyzer (model Li-7500; Li-Cor, Inc., Lincoln, NE, USA). Data were retrieved using a control system (model CR5000; Campbell Scientific, Inc., Logan, UT, USA) at a frequency of 10 Hz. Data were checked, and instruments were maintained weekly, which confirmed that we obtained a nearly continuous 10 year data series (October 2002 to October 2012).

[9] Quality assessment and control have been carried out on the eddy flux system, the details of which are provided in a previous publication [*Tan et al.*, 2010]. Net ecosystem carbon exchange (NEE) was calculated as the sum of the eddy and storage fluxes. Three-dimensional rotation of the coordinates was applied to the wind components to remove the effect of instrument tilt and irregularity on the airflow.

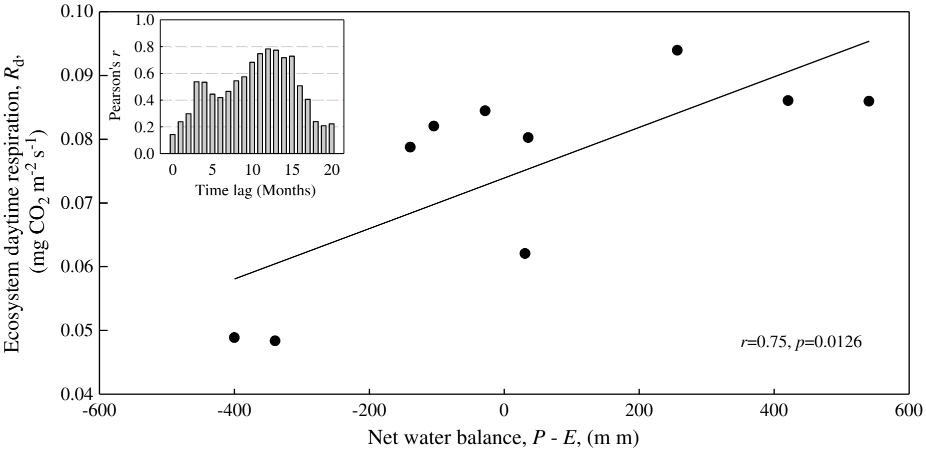

Figure 4. Daytime ecosystem respiration in relation to net water balance, with a time lag of 12 months. The subpanel shows how the Pearson's correlation between these two variables changed with the lag of time.

The flux data were also corrected for variability in air density caused by transfer of heat and water vapor. The infrared analyzer was calibrated yearly. In consistent to micrometeorological convention, here we defined negative values of NEE as net carbon uptake (carbon sink) (Figure 1).

[10] The eddy flux method has been criticized for uncertainty in its nighttime measurements. This is especially obvious in tropical areas, where nighttime turbulence is not well developed. Nevertheless, daytime eddy flux is reliable, and a few questions have been raised about the use of daytime data to address ecological questions [*Goulden et al.*, 2006]. Convincing results can be obtained from daytime eddy flux measurements, which provide a nondestructive means of obtaining information on ecosystem-level gas exchange. In this study, we used the 10 year, continuous, 0.5 h daytime eddy flux data (defined as solar radiation $>$10 W/m^2) in two ways.

[11] 1. To conduct ecosystem-level light response analysis and derive related ecosystem physiological parameters, we used the Michaelis-Menten formula [*Falge et al.*, 2001] for light response (Table 1), i.e.,

$$\mathrm{NEE} = -\frac{\alpha \cdot I_s \cdot P_{\max}}{\alpha \cdot I_s + P_{\max}} + R_d$$

where α, $P_{\max}$, and R_d are fitted parameters that represent apparent quantum yield, net rate of light-saturated ecosystem photosynthesis, and daytime ecosystem respiration, respectively. I_s is light intensity—here the downward, shortwave radiation recorded by a sensor (Model CM11; Kipp & Zonen, Delft, Netherlands) mounted at the top of the tower, rather than photosynthetically active radiation (PAR). PAR sensors were not used here because of inevitable decay that would occur over a decade-long measurement period; solar radiation sensors are more stable than PAR sensors for long-term measurements. We also compared measurements of solar radiation obtained at the top of the tower with data obtained from a standard meteorological station located 3 km from the study site. There was no evidence of a decay trend in the measurements.

[12] 2. The use of midday NEE. Here midday NEE is defined as NEE collected under the condition of downward solar radiation $>$200 W/m^2. This usually occurred between 15:00 and 19:00 h. Measurements of solar radiation $>$200 W/m^2 can eliminate nonideal weather conditions (e.g., rainfall and fog), thus providing more precise results.

[13] In addition, the 10 year continuous data were measured using the same set of instruments by nearly the same group of individuals. Thus, the data are thought to be appropriate and reliable for analyses of interannual variability. The raw data of inventory and eddy flux are available by request from the corresponding author.

2.4. Climatic Data

[14] Climatic data were obtained from a standard meteorological station located 3 km east from our plot. This weather station provided daily records of rainfall amount; pan evaporation; mean, minimum, and maximum temperatures; solar radiation; hours of sunshine; relative humidity; and water vapor pressure. In addition, monthly records of the number of rainfall and fog days, and the duration of fog, have been provided since 1 January 1959. After comparison among annual rainfall (P), dry season rainfall, and annual rainfall minus pan evaporation ($P - E$), we found the best index for water condition at the ecosystem level to be $P - E$ (details shown in sections 3 and 4). We then related growth and ecosystem fluxes to $P - E$ without specific declaration in the study.

3. Results

3.1. Inventory

[15] We observed obvious decelerating RGR over the past 10 years based on 7 years of effective data in the tropical forest (Figure 2a). This declining growth trend could be attributed to either a decrease in rainfall or an increase in temperature (Table 1). The net water balance (rainfall minus evaporation) explained over 92% of the trend in RGR (Figure 2b), while dry season rainfall showed no correlation with RGR. Neither total annual hours of sunshine ($r = 0.61$, $p = 0.14$) nor total solar radiation ($r = 0.34$, $p = 0.44$) was significantly correlated to interannual RGR. Tree mortality was generally higher during dry years and lower during wet years; 2002 data represented an outlier (Figure 2c).

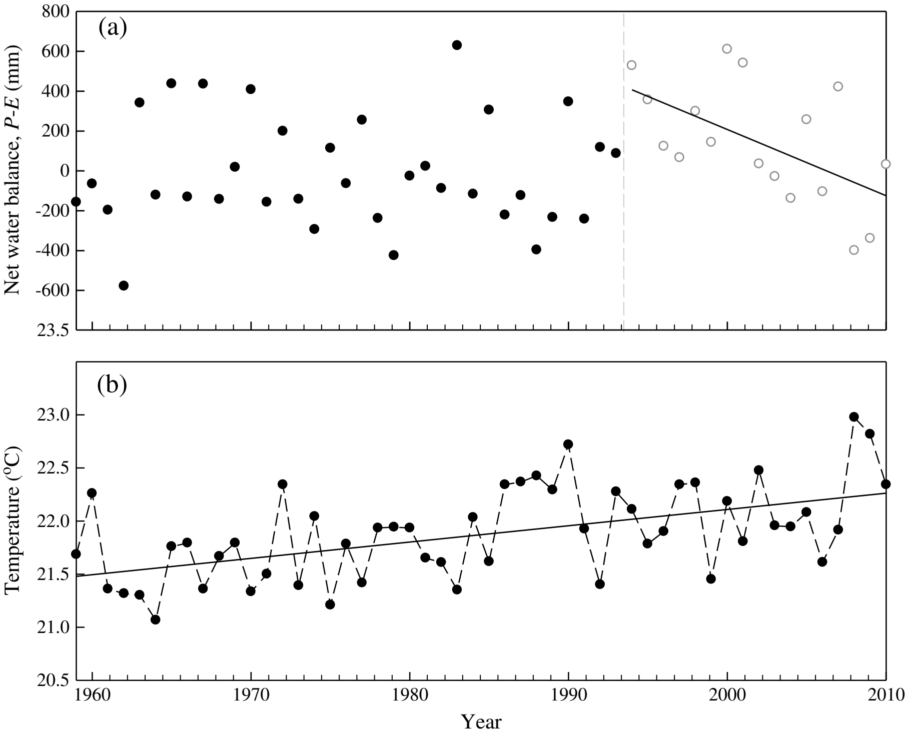

Figure 5. The (a) net water balance and (b) air temperature in the past half-century in Xishuangbanna, China. The net water balance during the inventory period was separated and passed through a Mann-Kendall trend test.

3.2. Eddy Flux

[16] Interannual variability in midday NEE was highly correlated to variability in net water balance, with the exception of 2011, which represented an outlier (Figure 3a). However, neither apparent quantum yield (α) nor saturated net ecosystem photosynthesis ($P_{\max}$) was correlated to water variability. In 2011, $P_{\max}$ values represented an outlier, but α values did not. The correlation between daytime ecosystem respiration (R_d) and net water balance changed with time lag and was only significant with a lag of 10–15 months (Figure 4).

3.3. Trends of Climatic Factors

[17] Air temperature was significantly (Mann-Kendall test, $p < 0.0001$) increasing at a rate of 0.158°C/decade (Figure 5b). No trend was observed for Xishuangbanna's rainfall or net water balance ($P - E$) during the past half century (Mann-Kendall test, $p = 0.2939$) (Figure 5a). However, during the most recent 17 year period of the inventory (1994–2010), a significant decrease in net water balance was detected ($p = 0.0189$).

4. Discussion

4.1. Decelerating Growth Trend Controlled by Water Variability

[18] Inventory data showed that the growth rate of the tropical rainforest studied here has decreased over the past 10 years (Figure 2a), a phenomenon that is inconsistent with the commonly suggested accelerating growth hypothesis (AGH). Midday net ecosystem photosynthesis derived from another independent method, eddy covariance flux, confirmed this trend (Figure 3a) and elucidated that reduced photosynthesis—rather than changes in carbon allocation—contributed to the deceleration in growth (Figures 3b and 3c). In contrast to results from Costa Rica [*Clark et al.*, 2003], net water balance, not temperature, was the main driver of this trend in our study site (Table 2). In the past, water variability, which does not show a trend as obvious as those of temperature or CO_2 (Figure 5b), has generally been ruled out as a factor accounting for growth trends in tropical forests. Over the long term—i.e., half a century to a century—no definitive trend was detected in rainfall time series. It is important to note that tropical rainfall usually oscillates in a periodic (approximately 20 years) cycle [*Malhi and Wright*, 2004], during which certain trends can be observed. Climate data from our study region provide a good example (Figure 5a). Rainfall observations from Costa Rica provide additional support for this perspective. Annual rainfall showed no significant directional changes ($r^2 = 0.002$) over a 49 year period of record, but there was a highly significant increase in rainfall ($r^2 = 0.42$, $p < 0.001$) during the most recent 24 years of the study period [*Clark and Clark*, 2011]. Thus, changes in availability of water could potentially influence growth trends in tropical rainforest as suggested by models [*Cox et al.*, 2000; *Cox et al.*, 2008]. Given predictions that tropical areas will experience increasingly dry conditions in the future [*Li et al.*, 2006; *Salazar et al.*, 2007], much more attention should be paid to the potential fate of the carbon sink in tropical rainforests.

Table 2. Pearson's Correlation (r) Between Mean Annual Relative Growth Rate (RGR) and Climatic Factors, and the Statistical Significance (p) of These Relationships in a Tropical Rainforest of Xishuangbanna, China[a]

Climatic Factor	Pearson's r	p
Total annual rainfall	0.91**	0.004
Total dry season rainfall	0.05	0.911
Annual rainfall minus evaporation	0.96**	<0.0001
Annual mean daily minimum temperature	−0.73	0.06
Annual mean temperature	−0.75*	0.05
Total annual hours of sunshine	0.61	0.14
Total annual solar radiation	0.34	0.44

[a] Single asterisks indicate statistical significance at the 0.05 level, and double asterisks indicate statistical significance at the 0.01 level.

4.2. Is There a Common Growth Trend for Tropical Rainforests All Over the World?

[19] Observational data from only one site are not sufficient to reject the AGH for tropical rainforests. Nevertheless, we can conclude that the CO_2 fertilization–induced accelerating growth hypothesis is not applicable as a common rule for all tropical areas—at least not for Xishuangbanna's tropical rainforest. We also question the existence of a common growth trend consistent among all tropical rainforests. Species composition, climatic environment, soil texture and fertility, and tree response and adaption to environmental perturbation could vary widely among tropical rainforests [*Davidson et al.*, 2012]. Regarding trends in tree growth in tropical rainforests, contrasting conclusions have been produced using the same method. Using tree inventory data from 14 large-scale tropical rainforest plots with a census interval of 5 years, *Chave et al.* [2008] claimed that there was no significant increase in biomass gain, which conflicts with the accelerating growth hypothesis; *Dong et al.* [2012] reported that tree growth could be well explained by solar radiation and nighttime temperature, where a mix of spatial and temporal observations was available. A decelerating growth trend was reported by *Feeley et al.* [2007] based on Barro Colorado Island (BCI) and Pasoh's inventory records. *Wagner et al.* [2012] reported that water condition was the main driver of tree growth in a tropical rainforest, based on short-term (approximately 4 years) but intensive measurements (2 month interval). The analysis of annual tree growth in Costa Rican rainforest found a decelerating trend in growth rate, which was attributed to an increase in daily minimum temperature but not to CO_2 concentration [*Clark et al.*, 2003, 2010]. As stressed by *Clark and Clark* [2011], annual inventory data are necessary in investigating the climatic controls on tropical rainforest tree growth. Given the necessity for tracking annual growth of tropical trees, and the paucity of attempts to do so, it is not appropriate for us to suggest a definitive conclusion regarding growth trends of tropical rainforests according to current data.

4.3. Time-Lagged Response of Ecosystem Respiration to Water Variability

[20] Pearson's correlation (r) between daytime ecosystem respiration (R_d) and net water balance changed with changes in time lag (Figure 4, subpanel). Ecosystem respiration is the sum of heterotrophic (R_h) and autotrophic respiration (R_a). R_h and R_a would respond to environmental perturbation differently. R_a is coupled to photosynthesis by the use of current photosynthates as substrates [*Hogberg et al.*, 2001]. Thus, the peak correlation that occurred at a time lag of 11–12 months was caused primarily by R_h. The sharp increase in correlation between net water balance and daytime respiration at 3 month time lag could be a result of an increase in seasonal drought-induced litterfall input. The climate of Xishuangbanna is strongly seasonal. The litterfall generated during the last dry season would be desiccated and would not decompose until the following rainy season. This phenomenon also could help to explain the long time lag between net water balance and daytime respiration in the Xishuangbanna rainforest studied here.

4.4. The Boom of Canopy Photosynthesis in 1 Year After a Severe Drought

[21] A reduction in net water balance largely weakened net ecosystem photosynthesis (Figure 3a) and thus slowed tree growth (Figure 2b). It is apparent that data from 2011 represent an outlier in the water-photosynthesis relationship (Figure 3a). In that year, the apparent light utilization (α) of the ecosystem—an index of light utilization efficiency under low radiation—was at normal levels (Figure 3c), while light-saturated net ecosystem photosynthesis ($P_{\max}$) was an outlier (Figure 3b). This indicates that the exceptionally high net ecosystem photosynthesis observed in 2011 was mainly a result of high $P_{\max}$, which itself could result from either high leaf-level photosynthetic capacity or a high leaf area index. Since leaf photosynthetic capacity is closely correlated with nitrogen content [*Wright et al.*, 2004] and production of new leaves requires nitrogen, the extra nitrogen that was apparently available in 2011. A severe drought (it is called a "one-in-a-century drought" by locals) occurred in the study region in 2009–2010, indicated by low net water balance in those years [*Qiu*, 2010]. The mortality rate increased from 1.5% for a normal year to 2.5% during the severe drought (Figure 2c). Severe drought also induced trees to shed more leaves [*Zhang et al.*, 2010]. We speculate that the boom of canopy photosynthesis in 1 year after a severe drought was caused by additional nutrient release [*Lodge et al.*, 1994].

[22] 1. A tropical rainforest is a nutrient-limited system [*Tanner et al.*, 1998].

[23] 2. Necromass would be accumulated during drought. On the one hand, much more litterfall input either from tree mortality or additional canopy leaf shedding. On the other hand, decomposition of necromass was suppressed by drought [*Saleska et al.*, 2003].

[24] 3. Accumulated necromass could be largely decomposed, while rainfall comes after drought. The released nutrients in decomposition subsequently will benefit canopy photosynthesis or tree growth [*Jarvis and Linder*, 2007; *Melillo et al.*, 2011].

[25] In other words, the exceptionally high photosynthesis that occurred in 2011 is a phenomenon of ecosystem recovery from a severe disturbance. In deserts, 2 years is required for an ecosystem to recover from drought [*Arnone et al.*, 2008]. In the tropical forest studied here, we did not observe exceptional ecosystem photosynthesis or respiration in 2012, after 1 year of recovery. It has shown the strong self-organization capacity of tropical rainforest at the same time [*Lin et al.*, 2009].

5. Conclusions

[26] We have made five conclusions.

[27] 1. A decelerating growth was observed in the studied rainforest during the past decade. The AGH was not supported by this study.

[28] 2. As another independent method, eddy flux observations confirmed that the observed growth trend was caused primarily by changes in canopy photosynthesis but not in carbon allocation.

[29] 3. The forest is highly sensitive to water variability, with low canopy photosynthesis, slow stand growth, and high mortality rates in dry years.

[30] 4. A boom of canopy photosynthesis in 1 year post drought was most probably a result of nutrient pulse caused by drought.

[31] 5. Ecosystem respiration was not correlated with net water balance within years, but significant correlations were found between these parameters with a time lag of 10–15 months.

[32] **Acknowledgments.** The funding support for this study includes the National Science Foundation of China (grants 31200347 and 41071071), the Western Light Project of CAS support to Z.-H. Tan, the Natural Science Foundation of Yunnan Province (grant 2011FB110), and the CAS 135 project XTBG-F01. Thanks to Xishuangbanna Ecological Station for support of field work and data management. Thanks to the individuals who participated in the field work over the past 10 years.

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