Cloud regulations on the gross primary productivity of a poplar plantation under different environmental conditions

<table>
<thead>
<tr>
<th>Journal:</th>
<th>Canadian Journal of Forest Research</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manuscript ID</td>
<td>cjfr-2016-0413.R1</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Article</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>16-Dec-2016</td>
</tr>
<tr>
<td>Complete List of Authors:</td>
<td>Xu, Hang; Beijing Forestry University, institute of soil and water conservation Zhang, Zhiqiang; Beijing Forestry University, College of Soil and Water Conservation Chen, Jiquan; Michigan State University, Landscape Ecology &amp; Ecosystem Science (LEES) Lab, Center for Global Change and Earth Observations (CGCEO), and Department of Geography Zhu, Mengxun; Beijing Forestry University, College of Soil and Water Conservation Kang, Manchun; Beijing Forestry University, institute of soil and water conservation; China Three Gorges University, College of Hydraulic and Environmental Engineering</td>
</tr>
<tr>
<td>Keyword:</td>
<td>cloudiness, gross primary productivity, poplar plantation, environmental conditions, path analysis</td>
</tr>
</tbody>
</table>

https://mc06.manuscriptcentral.com/cjfr-pubs
Cloud regulations on the gross primary productivity of a poplar plantation under different environmental conditions

Hang Xu¹, Zhiqiang Zhang¹, Jiquan Chen², Mengxun Zhu¹, Manchun Kang¹,³

¹. Key Laboratory of Soil and Water Conservation and Desertification Combating, Ministry of Education, College of Soil and Water Conservation, Beijing Forestry University, Beijing 100083, PR China

². Landscape Ecology & Ecosystem Science (LEES) Lab, Center for Global Change and Earth Observations (CGCEO), and Department of Geography, Michigan State University, East Lansing, MI 48823, USA

³. College of Hydraulic and Environmental Engineering, China Three Gorges University, Yichang 443002, PR China

Corresponding author: Dr. Zhiqiang Zhang (email: zhqzhang@bjfu.edu.cn).
Tel.: +86 10 62338097; fax: +86 10 62337873.
Abstract: Cloud regulates the gross primary productivity (GPP) of forest ecosystems by changing the radiation component and other environmental factors. In this study, we used an open-path eddy covariance system and microclimate sensors installed over a poplar plantation in northern China to measure the carbon exchange and climate variables during the mid-growing seasons (June to August) in 2014 and 2015. The results indicated that the GPP of the plantation peaked when the clearness index (CI) was between 0.45 and 0.65, at which point diffuse photosynthetically active radiation (PAR\textsubscript{dif}) had reached its maximum. Cloudy skies increased the maximum ecosystem photosynthetic capacity (P\textsubscript{max}) by 28% compared with clear skies. PAR\textsubscript{dif} and soil moisture were the most and the least crucial driver for photosynthetic productivity of the plantation under cloudy skies, respectively. The ecosystem photosynthetic potential was higher under lower vapor pressure deficit (VPD < 1.5 kPa), lower air temperature (T\textsubscript{a} < 30°C), and non-stressed conditions (REW > 0.4) for cloudy skies due to effects of T\textsubscript{a} and VPD on stoma. Overall, our research highlighted the importance of cloud-induced radiation component change and environmental variation in quantifying the GPP of forest ecosystems.

Key words: cloudiness, gross primary productivity, poplar plantation, environmental conditions, path analysis
1. Introduction

The global dimming phenomenon, caused by the drastic increase in clouds and atmospheric particulates produced by fossil fuel combustion and other human activities, has continuously decreased the amount of global solar radiation reaching the ground since the 1950s by 0.51 ± 0.05 W m$^{-2}$ yr$^{-1}$ (IPCC 2007; Wang et al. 2014). Despite this trend, there have been improvements for most areas of Europe and North America (Barnes et al. 2014), yet a sustaining decline in global radiation exists in the developing countries of the Northern Hemisphere (Streets et al. 2006; Wang and Yang 2014). Clouds and particulates can directly decrease total radiation while increasing diffuse radiation (Oliphant et al. 2011; Zhang et al. 2011), consequently affecting the growth and development of terrestrial ecosystems (Bai et al. 2012; Cheng et al. 2015).

Numerous studies have indicated that increased diffuse radiation under cloudy sky conditions can drastically enhance the gross primary productivity (GPP) of forest ecosystems and light use efficiency (LUE; defined as GPP/PAR) in regions that are not saturated with light (Kanniah et al. 2012, 2013; Cheng et al. 2015). On a global scale, the carbon sink of terrestrial ecosystems between 1960 and 1999 were estimated to increase by ~25% due to the increase in the diffuse fraction largely associated with the ‘global dimming phenomenon’ (Mercado et al., 2009). The underlying mechanisms for this increase are multi-fold; the increase in diffuse radiation can 1) lead to the removal of canopy photoinhibition in sunlit leaves (i.e., leaves above the canopy) at high levels of radiation under clear sky conditions (Gu et al. 2002; Knohl and Baldocchi 2008), 2) uniformly distribute the radiation in the canopy columns (Greenwald et al. 2006; Alton et al. 2007), and 3) stimulate plant stomatal opening, which is sensitive to the ratio of blue to red light (Dengel and Grace 2010).
Cloudiness and its temporal changes are often coupled with different environmental conditions, such as vapor pressure deficit (VPD), air temperature ($T_a$) and soil moisture (Kanniah et al. 2012, 2013), all of which produce complex, coupled effects on ecosystem photosynthesis and production (Cai et al. 2008). A few studies found that $T_a$ and VPD had no significant effects on controlling the ecosystem photosynthesis response to diffuse radiation (Jing et al. 2010; Kanniah et al. 2011; Oliphant et al. 2011), while other studies found that these factors played a crucial role (Yamasoe et al. 2005; Zhang et al. 2011). Yamasoe et al. (2005) reported that the increase in VPD under clear sky conditions could constrain carbon exchange in a tropical forest. Zhang et al. (2011) found that decreases in VPD and $T_a$ could depress canopy photosynthesis under cloudy skies in an irrigated maize cropland. Clearly, the significance of the radiation component and other environmental factors on ecosystem GPP remain unclear within these complex, interactive environmental conditions. Moreover, there are few studies that have quantified the effects of cloud-induced radiation components and other environmental factor changes on the ecosystem photosynthetic productivity of plantations. For example, recent studies based on a path analysis of the direct correlation between environmental factors and ecosystem GPP have demonstrated the complex nature of the above relationships (Shao et al. 2016).

Here, we hypothesized that the diffuse PAR ($\text{PAR}_{\text{dif}}$), mainly controlled by clouds, would be the dominant factor regulating forest ecosystem GPP under cloudy skies and that clouds would affect the GPP distinctively under different environmental conditions. To test the hypotheses, we used diurnal 30-min data ($\text{PAR} > 4 \mu\text{mol m}^{-2} \text{s}^{-1}$) collected during the mid-growing season (June to August) in combination with ancillary meteorological observations from an eddy covariance tower over a poplar plantation in northern China, to 1) quantify the cloudiness effect on ecosystem GPP and LUE, 2) explore GPP responses to cloudy skies under different environmental conditions.
environmental conditions, and 3) identify the direct and indirect effects of environmental
variables on ecosystem photosynthesis under various cloudy skies.

2. Materials and Methods

2.1 Site description

This study was conducted over a poplar plantation (*Populus × euramericana*) in Gongqing
Forest Farm (116°42′41″E, 40°06′27″N, 29 m a. s. l.), which is located on a fluvial plain near the
Chaobai River in Shunyi District, Beijing, China. The trees were planted in ~1996 at a density of
4 m × 3 m. The average height and diameter at breast height (DBH) of the plantation were 17.5 ±
1.6 m (mean ± SD) and 25.7 ± 1.6 cm, respectively, in 2014 and 2015. The leaf area index (LAI)
varied between 2.15 and 3.41 during the mid-growing season in 2014 and 2015. The understory
vegetation was dominated by *Swida alba Opiz.*, *Pinus bungeana Zucc.*, *Caryophylli Flos*,
*Sabina vulgaris*, and *Gaillardia aristata Pursh*. The region is typical of the sub-humid warm
temperate monsoon climate, with a mean annual temperature of 11.5°C and an average daily
temperature of 4.9°C in January and 25.7°C in July. According to the long-term (1990–2010)
meteorological Shunyi Weather Station (116°37′E, 40°08′N, 28.6 m a. s. l.), the mean annual
precipitation is ~576 mm, with 75% falling between July and September. The mean annual
relative humidity is 50% and the total hours of sunshine are ~690 h in the summer (i.e., June to
August). The soil texture is sandy with high permeability and a low water-holding capacity. The
ground water level during the study was ~2 m.

2.2 Fluxes and meteorological measurements

An eddy covariance (EC) system was installed on a 30 m tall tower in November 2013 to
continuously measure the exchange of carbon, water and energy between the plantation and the
atmosphere. An open-path gas analyzer (EC150, Campbell Scientific Inc., USA) and a 3-D sonic
anemometer (CSAT3, Campbell Scientific Inc., USA) were installed at 26 m with a north declination of 165° (i.e., the prevailing wind direction).

The global shortwave solar radiation (G), photosynthetically active radiation (PAR) and net radiation \( R_n \) were measured at the top of the tower (30 m) by a pyranometer (LI-200x, LI-COR Inc., USA), a light quantum sensor (LI-190SB, LI-COR Inc., USA), and a net radiometer (CNR1, Kipp and Zonen., NL), respectively. Two tipping-bucket rain gauges (TE525-L, Campbell Scientific Inc., USA) were mounted above the canopies to measure the cumulative precipitation over 30 min periods. Air temperature and relative humidity were measured at 0.5, 1.5, 5, 15 and 30 m above the ground using temperature and humidity sensors (HC2S3, Campbell Scientific Inc., USA), from which VPD was calculated. Soil moisture was measured by TDR (CS616, Campbell Scientific Inc., USA) at 5, 20, 50, 100, 150 and 200 cm below the soil surface. Soil temperature \( T_s \) and soil heat flux \( G \) were measured with two thermocouples (TCAV107, Campbell Scientific Inc., USA) and two soil heat transducers (HFT3, Campbell Scientific Inc., USA) installed at depths of 5 and 25 cm. All data were logged into CR3000/1000 dataloggers (Campbell Scientific Inc., USA) at 2/10 Hz. The leaf area index was measured twice a month using the plant canopy analyzer (LAI-2200, LI-COR Inc., USA).

2.3 Flux corrections and data processing

Eddypro (https://www.licor.com/env/support/) was used to process the 10 Hz raw data, including spike filtering, rotating the coordinates’ axis using the planar fit method (Foken et al. 2012) and WPL corrections (Webb 1982). Stationary and integral turbulent tests were performed (Foken 2006), splitting all data into 9 classes. The data of classes 9 and 8 with wind directions between > 350° and < 45° (north declination) were discarded because of insufficient turbulence and because they fell under the tower’s shade. The data with friction velocity below the threshold...
0.20 m s\(^{-1}\) for 2014 and 0.25 m s\(^{-1}\) for 2015 (Reichstein et al. 2005) were filtered out to eliminate the underestimation under stable stratifications. Simultaneously, the KM model was applied to remove data from beyond the study area (Kormann and Meixner 2001). With these quality controls and other system malfunctions (e.g., power failure, instrumentation malfunctioning and heavy rain conditions), 49% in 2014 and 52% in 2015 of data were finally reserved. Daytime gaps less than < 7 days were filled by using the marginal distribution sampling (MDS) approach (Reichstein et al. 2005). In addition, the larger gaps (i.e., more than 7 days) were filled by the mean diurnal variation (MDV) method with consecutive 15-day windows because the largest gap was less than 10 days (Krishnan et al. 2012).

The energy balance ratio (EBR), defined as effective energy/available energy, was 0.93 and 0.85 based on daytime 30-min fluxes in 2014 and 2015, respectively. Although there was energy storage in the canopy and air, our results were similar to the average value (0.84) of 173 FLUXNET sites (Stoy et al. 2013). We applied a non-linear regression method to calculate the ecosystem respiration (ER, i.e., nighttime NEE) and GPP (Lloyd and Taylor 1994) as follows:

\[
ER(t) = R_{ref} \cdot e^{E_{0,\text{short}} \left( \frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_{\text{soil}}(t) - T_0} \right)} 
\]

(1)

\[
GPP = ER - NEE
\]

(2)

where \(R_{\text{ref}}\) is the ER under the reference temperature, \(E_{0,\text{short}}\) denotes the activation energy parameter that determines the short-term temperature sensitivity (4 days in this study), \(T_{\text{ref}}\) is the reference temperature (10°C), \(T_0\) is a constant (-46.02°C) and \(T_{\text{soil}}\) is the soil temperature at 5 cm.

NEE is the net ecosystem exchange.

To compare the GPP responses to sky conditions under different environmental conditions, we divided the VPD into VPD < 1.5 kPa and VPD \(\geq\) 1.5 kPa (Zhou et al. 2013), \(T_a\) into \(T_a <\)
30°C and $T_a \geq 30°C$ (Kanniah et al. 2013) and relative extractable soil water (REW) into $\text{REW} < 0.4$ and $\text{REW} \geq 0.4$, representing soil water stress and non-stress, respectively (Granier et al. 1999). REW was calculated as follows:

$$\text{REW} = \frac{\text{VWC} - \text{VWC}_{\text{min}}}{\text{VWC}_{\text{max}} - \text{VWC}_{\text{min}}}$$

where $\text{VWC}_{\text{max}}$ and $\text{VWC}_{\text{min}}$ are the maximum and minimum soil moisture content measured at 5 cm.

### 2.4 Defining sky conditions

The clearness index (CI) that is the ratio of solar radiation ($G$) observed above the canopies to the extraterrestrial global horizontal solar radiance ($G_0$) (Kanniah et al. 2013), was used to represent the sky conditions (Gu et al. 2002) as follows:

$$\text{CI} = \frac{G}{G_0}$$

$$G_0 = G_{sc} \left[ 1 + 0.033 \cos \left( \frac{360d}{365} \right) \right] \sin \beta$$

where $G_{sc}$ is the solar constant ($1370 \text{ W m}^{-2}$), $d$ is the day of the year, and $\beta$ is the solar elevation computed by using the Solar Position Online Calculator operated by the National Renewable Energy Lab, USA (http://www.nrel.gov/mide/solpos/solpos.html).

A distinct CI threshold ($C_{It}$) to define the sky conditions cannot be found because CI changes not only with clouds and aerosol concentration but also with the variation of solar elevation (Gu et al. 1999). $C_{It}$ at a given solar elevation must be smoothly increased with $\sin \beta$ and form an envelope curve in the lumped scatter plot of $C_{It}$ against $\sin \beta$ (Gu et al. 1999). Due to the asymmetry between mornings and afternoons, we calculated the $C_{It}$ and its relationship with
\( \sin \beta \) separately (Fig. 1) with a cubic polynomial equation (Eq. 6) as follows:

\[
CI = a \sin^3 \beta + b \sin^2 \beta + c \sin \beta + d
\]

where \( a, b, c \) and \( d \) were estimated regression coefficients. Cloudy sky conditions were defined when \( CI \) was less than \( CI_t \) at a given solar elevation. To eliminate the effect of solar elevation on the relationship between ecosystem photosynthesis and \( CI \), we divided the 30-70° solar elevation data (\( \beta \)) into 5° intervals (Zhang et al. 2010; Bai et al. 2012).

### 2.5 Diffuse PAR

\( \text{PAR}_{\text{dif}} \) was calculated by using \( CI \) and solar zenith angle as (Reindl et al. 1991) follows:

\[
\text{PAR}_{\text{dif}} = \text{PAR} \times f_{\text{DPAR}}
\]

\[
f_{\text{DPAR}} = \frac{1 + 0.3(1 - q^2)}{1 + (1 - q)\cos^2(90 - \beta)\cos^3 \beta}
\]

\[
q = \frac{G_f}{G_0} \cdot CI
\]

when \( 0 \leq CI \leq 0.3 \); restrain \( G_f/G_0 \leq CI \),

\[
\frac{G_f}{G_0} = CI(1.020 - 0.254CI + 0.0123 \sin \beta)
\]

when \( 0.3 < CI \leq 0.78 \); restrain \( 0.1CI \leq G_f/G_0 \leq 0.97CI \),

\[
\frac{G_f}{G_0} = CI(1.400 - 1.749CI + 0.177 \sin \beta)
\]

when \( 0.78 < CI \); restrain \( G_f/G_0 \geq CI \),
\[
\frac{G_f}{G_0} = \text{Cl}(0.486\text{Cl} - 0.182\sin\beta)
\]

(12)

where fDPAR is the fraction of diffuse PAR and \(G_f\) is the diffuse fraction of the global solar radiation (W m\(^{-2}\)).

### 2.6 Light response model

The rectangle hyperbola light response model, known as the Michaelis-Menten equation, which can simulate the process of leaf and canopy level photosynthesis (Michaelis and Menten 1913), is widely used for quantifying the effects of cloudiness on ecosystem photosynthesis under different sky conditions. The formula is as follows:

\[
GPP = \frac{\alpha \text{P}_{\text{max}} \text{PAR}}{\alpha \text{PAR} + \text{P}_{\text{max}}}
\]

(13)

where \(\alpha\) is the ecosystem apparent quantum yield and \(\text{P}_{\text{max}}\) is the maximum ecosystem photosynthetic capacity (\(\mu\text{mol m}^{-2}\text{s}^{-1}\)).

### 2.7 Statistical analysis

We developed our path coefficient model by focusing on the interactive environmental factors, including \(\text{PAR}_{\text{dif}}\), direct PAR (\(\text{PAR}_{\text{dif}}\)), VPD, \(T_a\) and REW, to identify their direct and indirect effects on the GPP of the plantation under different environmental conditions. In simplifying the model structure, we only accepted the significant paths (\(p < 0.05\)) and standardized path coefficients (\(\rho\)) that were out of the range of -0.1 to 0.1. All observed data were standardized before putting into the path model, and the \(\rho\) and discrepancy were calculated based on the maximum likelihood method (Shao et al. 2016). The final models were adopted when the comparative fit index (CFI) was more than 0.9 and the root mean square error of approximation (RMSEA) was less than 0.05 (Kline 2011). The path analysis and data conversion were applied
within AMOS (version 24.0, Chicago, IL). All selected regression curves were statistically significant ($p < 0.05$) and based on several related studies (Zhang et al. 2010, Oliphant et al. 2011, Bai et al. 2012, Kanniah et al. 2013), which were conducted by SigmaPlot (version 12.5, California, USA).

3. Results

3.1 Microclimate and CI

The variations in the mean daily CI, REW, $T_a$, VPD, and daily total global solar radiation (G), daily total precipitation (P) during the mid-growing season of 2014 and 2015 were shown in Fig. 2. The mean daily CI in 2014 was $0.41 \pm 0.141$ (mean $\pm$ SE), which was greater than that in 2015 ($0.36 \pm 0.133$). Total daily G showed consistent changes, corresponding to the change in CI (Fig. 2c/d). The mean daily G in 2015 ($16.4 \pm 0.59$ MJ m$^{-2}$) was less than that in 2014 ($17.0 \pm 0.53$ MJ m$^{-2}$). The total G values during the same period from 2014 and 2015 were 1561.9 MJ m$^{-2}$ and 1507.3 MJ m$^{-2}$, respectively. The total rainfall during the mid-growing season of 2014 was 200.6 mm, 54% less than the long term average (432.1 mm) (Fig. 2a/b). As a result, the plantation experienced 68 days of soil water stress (REW < 0.4). In contrast, the rainfall in 2015 was 439.4 mm, resulting in 53 days of drought stress. The mean air temperature ($T_a$) during the mid-growing season in 2015 ($27.9 \pm 0.07^{\circ}C$) was lower than that in 2014 ($28.1 \pm 0.09^{\circ}C$) (Fig. 2e/f). The maximum mean daily $T_a$ of 2014 and 2015 was 30.8°C and 33.2°C, respectively, with both occurring in July. During the study period, $T_a$ under clear sky conditions ($29.6 \pm 0.23^{\circ}C$) was 8% higher than that of cloudy sky conditions ($27.1 \pm 0.08^{\circ}C$). The mean daily VPD in 2015 was $1.6 \pm 0.02$ kPa, which was lower than that in 2014 ($1.8 \pm 0.03$ kPa). The low $T_a$ and high P in 2015 resulted in a lower VPD than that in 2014.

In addition, sky conditions indicated by CI during the mid-growing seasons of two years
were related to the changes in VPD, $T_a$, PAR and PAR$_{dif}$ (Fig. 3). VPD, $T_a$ and PAR linearly increased with increasing CI ($p < 0.05$), however, the variation in PAR$_{dif}$ against CI presented a downward-parabolic trend under selected solar elevations during the study period. Sensitivities of environmental factors (i.e., the slopes of lines) to CI were higher under the solar elevations of 65-70° compared to the solar elevations of 45-50°, similarly, higher coefficients of determination were also found at higher solar elevations.

### 3.2 GPP and LUE against CI

The variations in the GPP to CI were conic across all ranges of $\beta$ in the study period (Fig. 4). The GPP peaked when CI ranged between 0.45 and 0.65 and was reduced when the skies were more cloudy or sunny. The mean diurnal GPP rate under cloudy sky conditions ($21.93 \pm 0.744 \mu\text{mol m}^{-2} \text{s}^{-1}$) in two years was higher than that in clear skies ($20.01 \pm 1.386 \mu\text{mol m}^{-2} \text{s}^{-1}$). More pronounced changes in the GPP against CI were observed at relatively higher solar elevations, demonstrating that ecosystem GPP enhanced more by cloudiness at higher solar elevations. In addition, LUE linearly increased with cloudiness among the solar elevations (Fig. 5) and was more efficient under cloudy skies ($0.054 \pm 0.001 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{PAR}$) than under clear skies ($0.048 \pm 0.006 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{PAR}$).

### 3.3 Light response under different sky conditions

The canopy photosynthetic productivity responded differently to PAR for clear and cloudy skies (Fig. 6). The apparent quantum efficiency ($\alpha$) was $\sim9\%$ lower under cloudy skies ($0.106 \pm 0.003 \mu\text{molCO}_2 \mu\text{mol}^{-1} \text{PAR}$) than that under clear skies ($0.117 \pm 0.009 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{PAR}$), while ecosystem photosynthetic potential ($P_{\text{max}}$) was elevated by 28% under cloudy sky conditions ($41.51 \pm 0.684 \mu\text{mol m}^{-2} \text{s}^{-1}$). Furthermore, with a lower $T_a$ ($T_a < 30^\circ$C) and VPD (VPD < 1.5 kPa), the $P_{\text{max}}$ of the plantation was increased by 30% and 33% due to the cloudiness (Fig. 7),
respectively. These increase rates were higher than that under higher VPD and Ta groups. In addition, Pmax was more sensitive to clouds under non-stressed conditions compared with water stress conditions (Fig. 7). Under cloudy sky conditions, the Pmax value was 33% higher for VPD < 1.5 than that for VPD ≥ 1.5, 12% higher for Ta < 30°C compared with that for Ta ≥ 30°C, and 29% higher for non-stressed soil than that for water stress soil. Our results indicated that lower VPD, lower Ta and non-stressed REW further promoted the ecosystem photosynthetic potential under cloudy skies.

3.4 Direct and indirect influences of environmental factors on GPP

There were different standardized path coefficients from climate variables to ecosystem photosynthetic productivity (Fig. 8). PARdif was the most important driver for ecosystem GPP under all environmental conditions, with ρ hardly changing with the variation of environmental groups (ρ = 0.54-0.65). Interestingly, soil REW was irrelevant to the GPP across all groups. Ta and direct PAR (PARdir) played positive roles (i.e., ρ > 0) on the GPP, while VPD suppressed ecosystem photosynthesis in most cases.

An environmental variable had different direct effects on GPP under different environmental conditions. The variation of path coefficients between radiation (i.e., PARdif and PARdir) and GPP was minimal while the variation between VPD and GPP was maxed (ρ = -0.52-0) among the environmental groups. A non-correlation between VPD and GPP was found when VPD was lower than 1.5 kPa. In addition, the influence of VPD on GPP under higher VPD (VPD ≥ 1.5 kPa) and higher Ta (Ta ≥ 30°C) conditions was more negative than that under lower VPD and lower Ta.

VPD depressed photosynthesis more severely under soil water stress conditions than non-stressed periods, and Ta was more relevant to GPP when it was lower compared to higher, while there were no discrepancies within the other environmental groups.
The indirect effects of $T_a$ on GPP were negative, indicating that the increase in $T_a$ would indirectly lead to the decrease in GPP via increasing VPD. There were more significant indirect effects under higher VPD (-0.32) and water-stress free conditions (-0.41) compared to lower VPD and water stress conditions. Similarly, the indirect effects of $T_a$ on GPP under high $T_a$ conditions (-0.26) were less than that (-0.14) under low $T_a$. Consequently, the total effects (i.e., sum of direct and indirect effects) of $T_a$ on GPP were positive only under lower VPD, lower $T_a$ or non-stressed conditions.

4. Discussion

4.1 Effects of cloudiness on GPP

Moderate cloud coverage (0.45-0.65) and corresponding diffuse radiation fractions between 0.50 and 0.80 presented optimal conditions that enhanced ecosystem productivity in the poplar plantation. Similar results were also observed within a temperate broadleaf forest in North America (Oliphant et al. 2011) and a temperate broadleaved pine forest in Northwestern China (Zhang et al. 2010). However, Kanniah et al. (2013) found that GPP rate was highest under clear sky conditions in a tropical savanna. Radiation component changes and light distribution within an ecosystem influences the canopy’s photosynthetic productivity under cloudy sky conditions (Knohl and Baldocchi 2008). Leaf area index and leaf orientation/arrangements within canopies are the primary factors determining scattered radiation usage in an ecosystem (Greenwald et al. 2006; Kanniah et al. 2012). Leaf inclination angles of the sunlit leaves of the poplar plantation were less than those of the sunshade leaves, which utilizes direct light and diffuse light simultaneously (Dickmann et al. 1990).

Ecosystem LUE consistently increased with cloudiness without any discrepancy among the solar elevations ($p > 0.05$) (Fig. 5), which further demonstrates the positive effects that
Cloudiness has on GPP. Cloudiness reduced the direct PAR for sunlit leaves and increased the 
PAR$_{\text{dif}}$ for shade leaves. These changes in PAR will reduce photosynthesis in the canopy’s sunlit 
foliage (within the photo prohibition range) but elevate the GPP of the shade leaves. Shade 
foliage and understory plants received more radiation to enhance their LUE and GPP (Alton et al. 
2007; Kanniah et al. 2011). As total radiation continued to decline against cloudiness, ecosystem 
GPP began to decrease because the radiation on the sunlit leaves was less than the light 
saturation point (Fig. 6). The reduction in GPP could not be compensated by the enhanced 
photosynthesis within the shade foliage or understory plants, which benefited from the diffuse 
radiation (Misson et al. 2005). Our data showed that cloudiness had strong effects on the 
plantation’s GPP and LUE, and that while LUE was enhanced by cloudiness, it could not lead to 
an increase in ecosystem GPP under conditions dominated by scattered radiation (i.e., fDPAR > 
0.5) in this plantation.

### 4.2 Effects of CI on environmental factors

Canopy GPP and other physiological processes were jointly influenced by multiple 
environmental factors, such as radiation, VPD, air temperature and soil moisture status (Yuan et 
al. 2009; Tian et al. 2011). $T_a$ linearly decreased with CI (Fig. 3c) due to reduced incident 
radiation (Gu et al. 1999). Likewise, VPD was lowered by cloudiness (Fig. 3a). Overall, clouds 
lowered leaf temperature and increased air humidity, thus reducing VPD. Although VPD, $T_a$ and 
PAR decreased with cloudiness for selected solar elevations ($p < 0.05$), the changes in 
environmental factors could not be well interpreted by CI at a lower solar elevation, indicating 
that the decrease in VPD and $T_a$ at a lower solar elevation was not solely attributed by cloudiness. 
This result might be due to the strong positive correlations between VPD, $T_a$ and solar elevations 
($p_{\text{VPD}} < 0.001$, $p_{T_a} < 0.001$). Under clear sky conditions, CI increased with sunrise (Perez et al.
1990; Misson et al. 2005). Thus, the decrease in VPD and $T_a$ with decreasing CI was partly induced by the decline in solar elevations at lower solar elevations. Unlike the linear relation of PAR with CI, the PAR$_{dif}$ was non-linearly correlated with CI (Fig. 3d), as indicated by previous studies (Alton et al. 2007; Zhang et al. 2011). PAR$_{dif}$ initially increased with the increase in CI and peaked until CI reached 0.40–0.60, and PAR$_{dif}$ declined afterwards in accordance with GPP (Fig. 4). Thus, PAR$_{dif}$ played a crucial role in controlling and regulating the plantation’s GPP under cloudy skies.

4.3 Environment regulations on GPP under different conditions of cloudiness

Cloudiness induced variations in radiation components and other environmental factors that led to interactive effects on forest ecosystem productivity. Our path analysis results showed that PAR$_{dif}$ was the primary factor under cloudy skies controlling photosynthesis in this fast-growing polar plantation, with no obvious discrepancy for the environmental groups (Fig. 8). This indicated that PAR$_{dif}$ did not cause the obvious difference in GPP between clear and cloudy skies under lower VPD, lower $T_a$ and non-stressed periods. The increase in VPD limited the poplar’s photosynthesis under different environmental conditions because leaf guard cell behavior is highly controlled by the balance of vapor pressure inside and outside of leaves (Farquhar and Sharkey 1982) and tends to be closed (i.e., decrease stomatal conductance) when there is an increase in VPD (Zhou et al. 2013; Goodrich et al. 2015). The sensitivity of ecosystem photosynthesis to VPD varied by environmental conditions (Day 2000). The discrepancy is due to the degree of deficit in CO$_2$ and H$_2$O for leaf photosynthesis. $T_a$ directly played a positive role in ecosystem photosynthesis because increased $T_a$ enhanced enzyme activity and photosynthetic electron transfer efficiency (Berry and Bjorkman 1980), which the poplar plantation could have used to promote leaf stomatal conductance, transpiration rates, and higher photosynthetic rates.
Additionally, increases in $T_a$ also resulted in increased VPD, leading to the indirect depression of ecosystem photosynthesis except for lower VPD conditions. These results confirmed that the regulation of ecosystem photosynthesis by environmental factors was complicated and coupled. Moreover, poplar species consume large quantities of water and are usually sensitive to soil water content (Kang et al. 2015). However, REW appeared to have been the least important factor for GPP under any environmental conditions likely because the taproots of the plants absorbed deep soil water in this plantation’s sandy soil, where sufficient underground water exists during water stress periods (Comas et al. 2013; Su et al. 2014).

Furthermore, there might have been a lagged photosynthesis response to the changes in soil water content, which lowers the correlation strength (Jia et al. 2014).

Correlation coefficients of the environmental factors among the different groups indicated that the GPP increase in varying degrees by cloudiness was directly ascribed to the discrepancy in the total effects of $T_a$ (i.e., the balance between negative effects of VPD and positive effects of $T_a$) on leaf stoma rather than the effects of PAR$_{dif}$ (Fig. 8). Clearly, the role of each environmental factor in regulating GPP and photosynthesis needs to be understood in the context of other variables, including cloudiness.

5. Conclusions

Cloudiness induced changes in radiation components while other environmental factors had coupling effects on the GPP of a fast-growing poplar plantation in northern China. The GPP of the plantation peaked with a CI of 0.45-0.65 when diffuse radiation was the largest component of the total solar radiation. Clouds increased ecosystem $P_{max}$ and LUE, leading to the continuous increase of canopy GPP until scattering radiation dominated. Our path analysis indicated that PAR$_{dif}$ was the most crucial driver while soil moisture was the least important factor for
photosynthetic productivity of the poplar plantation under cloudy sky conditions. In addition, lower VPD (VPD < 1.5 kPa), lower $T_a$ ($T_a < 30^\circC$) and non-stressed conditions ($REW > 0.4$) were more conducive to enhancing ecosystem photosynthesis under cloudy skies due to the comprehensive effects of VPD and $T_a$ to stomatal conductance. Therefore, evaluating the cloudiness effects for quantifying the GPP of forest ecosystems is important. Although we quantified the direct and indirect environmental effects on GPP under cloudy skies, the weakness of path analysis was that empirical relationships between ecosystem GPP and environmental factors were only considered. Thus further studies focusing on more biophysical processes should be conducted to explore more accurately the cloud effect on forest ecosystem productivity.

**Acknowledgments**

This study was financially supported by the Beijing Education Commission Grant to jointly support the Universities of Ministry of Education in Beijing and the National Special Research Program for Forestry, which was entitled “Forest Management Affecting the Coupling of Ecosystem Carbon and Water Exchange with Atmosphere” (grant no. 201204102). The fourth author also acknowledges the financial support of the Beijing Municipality Educational Committee under the graduate student training program. Partial support by the US–China Carbon Consortium (USCCC) is also acknowledged. The authors thank Gabriela Shirkey for editing the manuscript for language.
References


Granier, A., Bréda, N., Biron, P., and Villette, S. 1999. A lumped water balance model to evaluate duration and


Fig. 1. The change of the clearness index under clear skies (CIt) with the sin of solar elevation (sinβ) from June to August in 2015.

\[ y = -0.006x^3 - 0.412x^2 + 0.884x + 0.204, R^2 = 0.90, p < 0.0001 \]

\[ y = 0.208x^3 - 0.386x^2 + 0.468x + 0.434, R^2 = 0.65, p < 0.0001 \]
Fig. 2. Variation of environmental factors during the mid-growing season in 2014 and 2015. Daily precipitation (P) and relative extractable water (REW) (a/b); mean daily clearness index (CI) and daily total global solar radiation (G) (c/d); mean daily air temperature (Ta) and vapor pressure deficit (VPD) (e/f).
Fig. 3. Changes of vapor pressure deficit (VPD) (a), air temperature (Ta) (b), photosynthetically active radiation (PAR) (c) and diffuse photosynthetically active radiation (PARdif) (d) with clearness index (CI) for selected intervals of solar elevation during June to August in 2014 and 2015.
Fig. 4. Relationship between gross primary productivity (GPP) and the clearness index (CI) at different selected solar elevations from June to August in 2014 and 2015.
Fig. 5. Relationship between light use efficiency (LUE) and the clearness index (CI) at different selected solar elevation from June to August in 2014 and 2015.

Fig. 5
169x145mm (300 x 300 DPI)
Fig. 6. Ecosystem photosynthesis-radiation relationship of the plantation under different sky conditions from June to August in 2014 and 2015.

\[
\text{GPP} = 0.106 \times \frac{41.51}{(0.106 \text{PAR} + 41.51)}, \quad R^2 = 0.58
\]

\[
\text{GPP} = 0.117 \times \frac{30.08}{(0.117 \text{PAR} + 30.08)}, \quad R^2 = 0.52
\]
Fig. 7. The growth rate of canopy photosynthetic potential capability (Pmax) (µmol m\(^{-2}\) s\(^{-1}\)) under cloudy sky conditions versus clear sky conditions. Numbers above bars show the growth percentage of Pmax by cloudy skies compared to the clear skies under different environmental classifications.

127x79mm (300 x 300 DPI)
Fig. 8. The direct and indirect effects of environmental factors on ecosystem photosynthetic productivity (GPP) for different levels of vapor pressure deficit (VPD) (a/b), air temperature (Ta) (c/d) and relative extractable water (REW) (e/f) under cloudy skies during the study period. The values beside the paths are standardized path coefficients ($\rho$: -1-1), ‘$\rho < 0$’ denotes negative correlation and ‘$\rho > 0$’ denotes positive correlation.

Fig. 8
170x219mm (300 x 300 DPI)