Effects of forestry management and environmental factors on water and light use efficiencies in a cool-temperate mixed forest in northern Japan

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Abstract

Over a period of 9 years covering both disturbed and undisturbed periods, we evaluated long-term variations in water and light use efficiency (WUE, LUE) in a cool-temperate mixed forest in northern Hokkaido, Japan: our study clarified the relationship of WUE and LUE to environmental and vegetation variables. WUE and LUE markedly decreased after deforestation: they were negatively correlated with the seasonal variations in photosynthetically active radiation (PAR) and water vapor deficit, and LUE increased with the increase in the leaf area index (LAI) coincident with the vegetation recovery. Other environmental and vegetation variables did not explain the changes in the WUE and LUE. The effect of clear-cutting on LUE was well explained by the change in the LAI; on the other hand, vegetation composition (developed forest or young tree seedling with dense undergrowth) had little effect on the magnitude and variation of LUE. In contrast, the change in LAI had little effect on WUE, because WUE is more sensitive to the atmospheric water deficit than it is to vegetation structure.

Key words: Clearcut, Evapotranspiration, Gross primary production, Larch, Sasa

1. Introduction

Vegetation plays a key role in the ecosystem carbon, water, and energy cycles (Roupard et al., 2009; Niu et al., 2011). The energy cycle is linked to the carbon balance through photosynthesis and to the water cycle by transpiration; the stomatal pathway controls both CO₂ and H₂O conductance. Two indices can express these relations: water use efficiency (WUE), defined as the ratio of gross primary production to evapotranspiration (GPP/ET), and light use efficiency (LUE), defined as the ratio of GPP to photosynthetically active radiation (GPP/PAR). Understanding the seasonal dynamics of WUE and LUE may improve our knowledge of the relationship between carbon, water, and energy cycles (Zhu et al., 2014). In addition, LUE can be an effective means to create a simple model (e model: Monteith, 1972) using remote sensing data to estimate large-scale ecosystem productivity (Lagergren et al., 2005); WUE can provide an index to specify the ecosystem water use strategy for survival of plants. This knowledge can be useful for managing water in agriculture and forestry.

WUE and LUE are usually controlled by many factors, such as vegetation type of the ecosystem, growth stage, and other environmental factors such as climate and soil. Monson et al. (2010) concluded that canopy structure explains the differences in WUE among forest ecosystems in high-elevation subalpine forests. Jassal et al. (2009) reported that WUE increases with the age of young forests, whereas it remains roughly constant for older forests in Pacific Northwest Douglas-fir stands. LUE increases under widely scattered radiation (Lamaud et al., 1996; Rocha et al., 2004), and decreases as the water vapor deficit increases (Baldocchi et al., 1987).

WUE and LUE change with forest growth stages, and these growth stages are altered by disturbances such as deforestation, windthrow, insect damage, and forest fire. For example, Mkhabela et al. (2009) showed that the WUE increased in direct proportion to the recovery time after fire and harvesting in Douglas-fir stands on Vancouver Island. However, the effects of disturbance on WUE and LUE in ecosystems or their long-term transformation after the disturbance have been reported by only a few studies. At the ecosystem level, the effects may be reduced due to the dominance of fast-growing herbaceous plants. We evaluated WUE and LUE variation over 9 years covering both undisturbed and disturbed periods in a cool-temperate forest in northern Hokkaido, Japan, and we clarified their relationship with the vegetation structure and meteorological variables.

2. Methods

2.1 Site description and forestry management

The measurements were conducted in Teshio experimental forest of Hokkaido University in northern Japan (45°03’N, 142°06’E, 66 m a.s.l.). The mean annual precipitation is about 1200 mm, and the mean temperature is 16.1 °C in August and −7.5 °C in January. The study site is located on a plateau in the experimental forest. Before deforesting, the forest was mixed, composed of Betula platyphylla Scat. var. japonica (Mich.) Hara, Betula ermanii Cham., Quercus crispula Blume, Picea glehni (F. Schmidt) Mast., and Abies sachalnensis (F. Schmidt) Mast., with the average canopy height of about 20 m (Aguilos et al., 2014); the forest floor was covered with relatively short...
(1.5 m), dense, evergreen dwarf bamboos (Sasa bamboo: *Sasa senanensis* (Franch. et Sav.) Rehder), partly coexisting with *Sasa kurilensis* (Rupr.) Makino et Shibata.

The trees in one area of the experimental forest (13.7 ha) were clear-cut between January and March 2003, removing about half (1203 m²) of the tree biomass (2193 m³). *Sasa* bamboo was kept intact under the snowpack during the operation; however, in October 2003 the bamboo in the clear-cut area was strip-cut into alternating 4-m-wide cut and uncut rows to provide space for the planting of 2-year-old hybrid larches (*Larix gmelinii* (Rupr.) Kuzen var. *japonica* (Maxim. Ex Regel) Pilg. × *Larix kaempferi* (Lamb.) Carrière) at a density of 2500 trees ha⁻¹. In the rows where *Sasa* had been strip-cut, *Sasa* weeding was conducted late in May, June, and July in 2004, and once in June of 2005 and 2006 to eliminate all *Sasa* growing between the larch trees. Weeding of *Sasa* ceased in 2007, because the larches had grown taller than the surrounding *Sasa* and thus could receive enough solar radiation to grow without shading.

### 2.2 Eddy flux and other meteorological measurements

The CO₂, H₂O, and sensible heat fluxes over the mixed forest were measured by a closed-path eddy covariance system established in August 2001 at a height of 32 m. A sonic anemometer (DA6003TV; Kajio, Tokyo, Japan) and an infrared-gas analyzer (IRGA) (LI-7000; Li-Cor, Inc., Lincoln, NE, USA) were used to evaluate the fluxes (Takagi et al., 2009; Aguilos et al., 2014). Fluctuation data of wind speed, air temperature and CO₂/H₂O concentration were sampled at 10 Hz with a digitizing data recorder (DRM3, TEAC Corp., Tokyo, Japan, until October 2003; CR5000, Campbell Scientific, Logan, UT, USA, from October 2003) after low-pass filtering with a cut-off frequency of 5 Hz. After clear-cutting, in addition to the continuous flux monitoring at 32 m, an open-path eddy covariance system was installed at a height of 4.6 m in June 2003 and was replaced by a closed-path system in October 2003. In the open-path system, a sonic anemometer (DA6003TV) measured 3-D winds and temperature, and an IRGA (OP2; Data Design Group, La Jolla, CA, USA) measured the molar fraction of CO₂ and H₂O to air. In the closed-path system, an LI-7000 IRGA (Li-Cor) was used and the measurement was continued until 2010, although the measurement height was raised to 5.7 m in May 2007 in accordance with the vegetation growth. CO₂ fluctuations were calibrated every day by using 2 standard gases (320 and 420 CO₂ μmol mol⁻¹), and H₂O fluctuations were calibrated by dynamic calibration (Takagi, 2012) using the H₂O fluctuations obtained by the slow-response humidity sensor (HMP45A; Vaisala, Helsinki, Finland). Flux values obtained at heights of 4.6 (or 5.7) m were used during nearly all of the period after the clear-cutting, except from January to May during and just after the clear-cutting, and in early October 2003, when no surface flux data were available.

Meteorological measurements at a height of 32 m included air temperature (*Tₐ*) and relative humidity (using the HMP45A sensor), wind speed and direction (010C and 020C; Met One Instruments, Grants Pass, OR, USA), net radiation (*Rn* (CRN-1; Kipp & Zonnen, Delft, the Netherlands), and photosynthetically active radiation (PAR; LI-1908SZ, Li-Cor, until May 2007; ML-020P; EKO Instruments Co., Ltd., Tokyo, Japan, from May 2007). These parameters were also monitored above the *Sasa* canopy (~2 m above the ground) using the same instrument types as those used at 32 m. Atmospheric pressure (PTB210-C6C5A; Vaisala) and rainfall (CYG-52202; RM Young, Traverse City, MI, USA) were also measured. The soil heat flux at a depth of 1 cm below the soil surface (*G*) and the soil water content (SWC) at 5 cm depth were measured at 5 points around the flux tower using soil heat plates (HFT-1.1; REBS, Seattle, WA, USA) and time-domain-reflectometry sensors (CS615; Campbell Scientific), respectively. The meteorological and soil data were sampled every 5 s, and data were stored as 0.5-h means or sums in two dataloggers (CR23X; Campbell Scientific) connected to a PC, which downloaded the logged data automatically.

### 2.3 Calculations of net ecosystem CO₂ exchange and evapotranspiration rates

The daily sonic rotation angle for use in the planar fit rotation (Wilczak et al., 2001) was determined with the 30-min mean wind speed in a 15-day moving window. For the closed-path system, the sonic-tube lag time for CO₂ and H₂O was determined monthly by averaging the lag times obtained at 30-min intervals under turbulent conditions. With these angles and lag times, half-hourly CO₂ (*Fₐ*, μmol m⁻² s⁻¹) and H₂O (ET, kg m⁻² s⁻¹) fluxes were calculated. We applied block averaging (30 min) but not trend removal to the 10 Hz fluctuation data when we calculated the covariance. Crosswind speed and water vapor concentration effects on the sensible heat flux were corrected by the methods of Kaimal and Gaynor (1991) and Hignett (1992), respectively. We then corrected the effect of air density fluctuations on the flux values (Webb et al., 1980; Leuning and King, 1992).

High-frequency losses for the sonic sensor’s span and sensor separation were corrected with transfer functions related to the sources of signal damping (Moore, 1986) for both open- and closed-path fluxes, and losses for tube attenuation were corrected following the method of Kowalski et al. (2003) only for the closed-path fluxes. Co-spectra between the vertical winds and the scalars (temperature and the concentrations of CO₂ and H₂O) were normalized by integrating the covariance over the band-pass range (0.003 to 0.01 Hz for CO₂ and 0.003 to 0.007 HZ for H₂O) and averaged over periods with a similar wind speed under turbulent conditions (Takagi, 2012).

Before the clear-cutting, net ecosystem CO₂ exchange (NEE, μmol m⁻² s⁻¹) was determined as the sum of *Fₐ* and *Fₐ*, where *Fₐ* is the change in CO₂ storage in the air column from the forest floor to the flux measurement height and was calculated from the observed CO₂ profiles measured at 4 (snow-covered period) or 5 (snow-free period) levels with an IRGA (DX6100; RMT Ltd., Moscow, Russia) (Takagi et al., 2009). After clear-cutting, *Fₐ* was used to represent NEE, because the night-time *Fₐ* was stable when the friction velocity (*u⁎*) exceeded 0.1 m s⁻¹.

All raw flux data were checked following the quality-control program proposed by Vickers and Mahrt (1997), and gaps in raw data caused by removal of noise spikes were filled by linear interpolation. The instationarity ratio and integral turbulence characteristic tests (Foken and Wichura, 1996) were applied to the 30-min averaged flux. Footprints of the observed CO₂
and H₂O fluxes were evaluated with the model developed by Kormann and Meixner (2001) to remove the effect of fluxes outside the clearcut. The cumulative footprint was evaluated every 30 min from the observation point in 1-m steps up to a distance of 2 km and up to the boundaries of the cut area (ranging from 140 to 340 m according with the wind direction). The flux data were removed if the ratio of 2 cumulative values was less than 0.7. Open-path Fₑ and ET during and just after (within 1 h) rainfall (> 0.5 mm 30 min⁻¹) were removed. Filtration by friction velocity (u*) was applied to the remaining NEE data: the threshold value was set at 0.3 m s⁻¹ for the forest and 0.1 m s⁻¹ for the clearcut. Because we used unified system for most of the study period (in 2002 and from Oct 2003 to 2010) and we evaluated the qualities and footprint of the fluxes every 30 min, we minimized the effect of the change in the system and the observation height on the observed fluxes. We could not observe any systematic drift owing to the change in the instrument or observation height.

NEE and ET obtained during the snow-free period (i.e., from May to October) were studied in this use. Gaps in the NEE and ET data were filled mainly with data from look-up tables (Falge et al., 2001). Look-up tables were created for every 30 days during snow-free periods each year. Air temperature and PAR were used as the environmental factors to create the look-up tables for NEE both before and after clearingcutting, whereas net radiation and atmospheric vapor pressure deficit were used for ET. Some data gaps that remained (<5% of the set of 30-min data in a year) after applying data from the look-up tables were filled using the mean diurnal variation approach (Falge et al., 2001), in which a missing flux value was replaced by the mean for that time based on the adjacent 9 days (4 days before and 5 days after that day). The few remaining gaps (<1% of the total) after the mean diurnal approach were filled by means of linear interpolation.

### 2.4 Calculations of GPP, WUE, and LUE

Night-time NEE (PAR < 1 μmol quantum m⁻² s⁻¹) was assumed to be equivalent to ecosystem respiration (RE) (i.e., GPP, assumed to be 0). During the snow-free period, the 30-min values of night-time NEE were compiled for air temperature classes (at 2 °C intervals), and the average NEE for each temperature class was related to the air temperature with the following equation (Lloyd and Taylor, 1994) for each year as shown in Takagi et al. (2009):

\[
RE = R_{ref} \times \exp \left[ \left( \frac{E_c}{R} \times \left( \frac{1}{T_{ref}} - \frac{1}{T} \right) \right) \right]
\]

where \(T_{ref}\) is the reference temperature (283.16 K), \(R_{ref}\) is the ecosystem respiration at the reference temperature (μmol m⁻² s⁻¹), \(E_c\) is the apparent temperature sensitivity (J mol⁻¹), \(R\) is the universal gas constant (8.314 J K⁻¹ mol⁻¹), and \(T\) is the air temperature at the canopy height (K). The constants \(R_{ref}\) and \(E_c\) were fixed throughout a given snow-free period, and daytime RE was estimated every 30 min with equation (1) and air temperature with determined \(R_{ref}\) and \(E_c\). Hourly GPP was estimated as RE–NEE.

WUE and LUE efficiencies used in this study are defined as

\[
WUE = \frac{\text{GPP}_{daytime}}{\text{ET}_{daytime}}
\]

\[
LUE = \frac{\text{GPP}_{daytime}}{\text{PAR}_{daytime}}
\]

where \(\text{GPP}_{daytime}\) (g CO₂ m⁻² daytime⁻¹ for WUE, and μmol CO₂ m⁻² daytime⁻¹ for LUE), \(\text{ET}_{daytime}\) (kg H₂O m⁻² daytime⁻¹), and \(\text{PAR}_{daytime}\) (μmol quantum m⁻² daytime⁻¹) are the sum of daytime GPP, ET, and PAR. The daytime was defined as the time from 8:30 to 16:30 LCT during which \(R_n > 0\). We used PAR observed at 32 m height throughout the study period. WUE and LUE with no data gap in GPP, ET, and PAR were used for the analyses. Different units were used for \(\text{GPP}_{daytime}\) to calculate WUE and LUE for each other, to facilitate easy comparison of the values with those from previous studies.

#### 2.5 Environmental and vegetation factors

Water vapor deficit at the mean evaporative surface (\(D_h\); kPa) was determined with the following equation (Kelliher et al., 1993):

\[
D_h = D - \left[ \frac{\Delta (\gamma + 1)}{0.622 G_c \rho} \right] (ET - E_{eq})
\]

where \(D\) is the vapor pressure deficit at the reference height (kPa), \(\Delta\) is the slope of the saturation vapor pressure–temperature curve at the mean wet-bulb temperature (kPa °C⁻¹), \(\gamma\) is the psychrometric constant (kPa °C⁻¹), \(P\) is the atmospheric pressure (kPa), \(G_c\) is the aerodynamic conductance (m s⁻¹), \(\rho\) is the air density (kg m⁻³), and \(E_{eq}\) is the equilibrium evaporation rate (kg m⁻² s⁻¹). Assuming neutral stability, \(G_c\) is calculated as

\[
G_c = \frac{\kappa^2 h}{\ln \left( \frac{z - d}{z_0} \right)}
\]

where \(\kappa\) is von Karman’s constant, \(\nu\) is the wind speed at measured height (z; m s⁻¹), \(d\) is the displacement height (m), and \(z_0\) is the roughness length (m) of the vegetation (Thom, 1975). The \(d\) and \(z_0\) were assumed to be 0.64 x \(h\) and 0.13 x \(h\), respectively (Campbell, 1977), where \(h\) is the vegetation height (m), for which 20 m and 1.5 m were used before and after the clear-cutting, respectively. The equilibrium evaporation rate \(E_{eq}\) is calculated as (McNaughton, 1976)

\[
E_{eq} = \frac{\Delta (R_n - G)}{1(\Delta + \gamma)}
\]

where \(I\) is the latent heat of vaporization of water (J kg⁻¹) and \(G\) is soil heat flux.

Canopy conductance \(G_c\) (m s⁻¹) was evaluated as a vegetation factor to explain the WUE and LUE variation: it represents stomatal openness at a canopy level and can be derived from the
reciprocal of canopy resistance in the Penman-Monteith equation (Monteith, 1965):

$$G_s = \frac{1}{\Delta (R_n - G_s) + \rho C_p D_s \gamma (\Delta + \gamma) / \gamma G_s}$$  \hspace{1cm} (7)

where $lE$ is the latent heat flux ($W \cdot m^{-2}$) and $C_p$ is the specific heat of air at constant pressure ($J \cdot kg^{-1} \cdot ^\circ C^{-1}$). Daytime (from 8:30 to 16:30 LCT and $R_n > 0$) average $D_s$, $G_s$, PAR, air temperature ($T_a$), and SWC were calculated to see their effects on LUE and WUE. $T_a$ and $D$ observed at 32 m height were used in 2002 for the mixed forest, whereas those at 2 m height were used from 2003 to 2010 for the clearcut. PAR observed at 32 m height was used throughout the study period.

The LAIs of young larches, other trees and Sasa were measured separately every 2 to 4 weeks during the snow-free season with a plant canopy analyzer (LAI–2000; Li–Cor). The LAI of each component was measured 3 to 5 times (2 reference values [no canopy shade] and 10 sample values [with canopy shade] for each measurement) and averaged, thus the LAI in this study includes the shade by the stems, branches, and culms in addition to the leaves of each canopy. In 2002 before clear-cutting, the total LAI in the study area was evaluated as the sum of forest and Sasa LAI. In 2003 just after the clear-cutting, total LAI was equal to that of former undergrowth Sasa because of the absence of canopy trees. The total LAI from 2004 to 2006 was evaluated as the average of Sasa LAI in the rows where Sasa remained and of larch LAI where Sasa was strip-cut. Sasa weeding stopped in 2007, and thus the total LAI from 2007 to 2009 was evaluated as the average of Sasa LAI where Sasa was left to grow and larch + recovering Sasa LAI in the rows where Sasa had been strip-cut. In 2010, 3 years after the last weeding, Sasa LAI in the strip-cut rows was almost equal to that in the surrounding uncut rows, blanketing all gaps between the trees. Thus, the total LAI was evaluated as the sum of larch and Sasa LAI.

### 3. Results and discussion

#### 3.1 Inter-annual and seasonal variations of GPP, ET, PAR, WUE, LUE, and LAI

The seasonal maximum of GPP occurred in July or August, whereas that of ET occurred during the period from July to September (Fig. 1). Both GPP and ET decreased after clear-cutting during 2003 and 2004, although the magnitude of the decrease was larger for GPP than for ET. The smaller effect of clear-cutting on ET than on GPP can be explained by the difference in their source and sink distribution in the ecosystem: the decrease in GPP and transpiration from the plant canopy after clear-cutting was due to the decrease in leaf area, whereas evaporation from the soil surface could have been enhanced by the increase in heat and wind exposure caused by the removal of canopy trees. GPP and ET recovered after 2005, and by 2010 their values had returned to almost the same level as those recorded before clear-cutting. PAR showed less inter-annual variation than GPP and ET and reached its seasonal maximum in the period from May to July.

LAI, WUE, and LUE markedly decreased in 2003 after the

![Fig. 1.](image-url)
clear-cutting (Fig. 2). LAI during the period 2004 to 2006 was lower than that in 2003 because of the strip-wise cutting of *Sasa*; indeed, LAI increased after the *Sasa* weeding stopped. The recovery of ecosystem LAI was mainly due to the contribution of *Sasa* bamboo.

Looking at further details, LUE gradually increased after 2003 and had recovered in 2010 to nearly the same level as LUE during 2002, before clear-cutting. That the inter-annual and seasonal variation of LUE seemed to correspond with the development of LAI suggests that the transition of vegetation type through forestry activities (developed forest or young tree seedlings with dense undergrowth) has only a small effect on the ecosystem LUE. However, WUE in 2010 was less than half of that in 2002; WUE recovered much more slowly than did LUE. Moreover, there was no apparent relationship between inter-annual and seasonal variation of WUE and LAI, suggesting that meteorological or other factors contributed to the variation in ET. Large WUE values were recorded in May and June 2007 (Fig. 2a). In this period of the year, there was a tendency that PAR was large and the saturation deficit was small (not shown). As a result, high photosynthetic rate was achieved with low evapotranspiration, and WUE was increased.

The annual average WUE values during the experimental period ranged from 11.84 (2003) to 31.95 (2002) g CO$_2$ kg H$_2$O$^{-1}$, and the annual average LUE values ranged from 9.15 (2003) to 21.17 (2010) µmol CO$_2$ µmol quantum$^{-1}$. The WUE values are higher than those obtained in beech forest (7–17 g CO$_2$ kg H$_2$O$^{-1}$; Herbst *et al*., 2002), deciduous temperate forest (4–15 g CO$_2$ kg H$_2$O$^{-1}$; Zhu *et al*., 2014), and evergreen subtropical forest (5–18 g CO$_2$ kg H$_2$O$^{-1}$; Zhu *et al*., 2014), and lower than those of aspen-dominated forest (20–60 g CO$_2$ kg H$_2$O$^{-1}$; Rocha *et al*., 2004). Our LUE values are in essentially the same range as those obtained in previous studies, for example, coconut plantation (18 µmol CO$_2$ µmol quantum$^{-1}$; Rouparsard *et al*., 2009), maritime pine forest (6–34 µmol CO$_2$ µmol quantum$^{-1}$; Lamaud *et al*., 1996), and Scot pine and Norway spruce forest (8–15 µmol CO$_2$ µmol quantum$^{-1}$; Lagergren *et al*., 2005).

### 3.2 Relationships of WUE and LUE with environmental and vegetation factors

WUE was well expressed as an exponential function, and LUE was also well expressed as a linear function of daytime average $D_0$ (Fig. 3). These negative relationships for WUE and LUE were also observed when they were plotted against daytime average PAR (Fig. 4). The coefficients of these regressions of WUE and LUE to $D_0$ (Table 1) and of WUE and LUE to PAR (Table 2), and their determination coefficients are summarized in Tables 1 and 2. The negative exponential relationships between $D_0$ and WUE are consistent with those of many previous studies (e.g., Baldocchi *et al*., 1987; Lamaud *et al*., 1996; Testi *et al*., 2008). For each experimental year, the determination coefficients for WUE and LUE to PAR were higher than those for WUE and LUE to $D_0$. The determination coefficients for WUE to PAR or to $D_0$ were the lowest in 2003, when LAI was lowest. These results were expected, as transpiration from a forest is closely coupled with atmospheric water vapor deficit of the upper air, whereas photosynthesis is relatively independent of that deficit (Baldocchi *et al*., 1987).

**Fig. 2.** Seasonal and inter-annual variation of monthly averages of (a) daytime average water use efficiency (WUE) and light use efficiency (LUE), and (b) ecosystem leaf area index (LAI). Downward arrows in (b) indicate the month that the strip-wise cutting for *Sasa* bamboo was conducted. For instructions on determining the ecosystem LAI, see the Methods section under “Environmental and Vegetation Factors.”
From the linear decrease of LUE with increasing PAR, GPP can be expressed as a quadratic function of PAR as $GPP = c_0 PAR^2 + c_1 PAR$; thus, there is a peak GPP value at $-c_1/2c_0$, representing the most efficient light condition for GPP. The

![Fig. 3.](image1.png)

**Fig. 3.** The relationship between (a) daytime average water use efficiency (WUE) and vapor pressure deficit at mean evaporative surface ($D_0$), and (b) daytime average light use efficiency (LUE) and $D_0$, where $D_0$ was bin-averaged by every 0.2 kPa. The regression lines, expressed as $WUE = a \exp(b D_0)$, and $LUE = c D_0 + d$, are shown in each panel, and the coefficients are listed in Table 1 with their coefficient of determination ($R^2$). The gray whiskers in these figures represent standard deviation.

![Fig. 4.](image2.png)

**Fig. 4.** The relationship between (a) daytime average water use efficiency (WUE) and photosynthetically active radiation (PAR), and (b) daytime average light use efficiency (LUE) and PAR, where PAR was bin-averaged every 100 $\mu$mol m$^{-2}$ s$^{-1}$. The regression lines, expressed as $WUE = a \exp(b PAR)$, and $LUE = c PAR + d$, are shown in each panel, and the coefficients are listed in Table 2 with their coefficients of determination ($R^2$). The gray bars in these figures represent standard deviation.
most efficient PAR calculated as $-d_v/2c_P$ was apparently low only in 2003 (daytime average PAR = 737 µmol m$^{-2}$ s$^{-1}$), just after the clear-cutting, compared with other years (from 922 to 1111 µmol m$^{-2}$ s$^{-1}$ with the average of 1026 µmol m$^{-2}$ s$^{-1}$ and the standard deviation of 54 µmol m$^{-2}$ s$^{-1}$). This suggests that the ecosystem light requirement was decreased by the clear-cutting and that the remaining vegetation did not fully use available PAR (maximum of daytime average PAR = 1600 µmol m$^{-2}$ s$^{-1}$). Moreover, the slope $c_P$ decreased and the y-intercept $d_v$ increased with the increase of the seasonal maximum LAI ($\text{LAI}_\text{max}$) (Fig. 5).

These relationships indicate that the dosage effect of LAI is exerted under low light conditions and is attenuated under high light conditions. That is, the light condition under the canopy was not as degraded regardless of LAI, presumably because of increased scattering radiation.

WUE decreased with the increase of daytime average $T_c$ in most of the experimental years (Fig. 6a). This tendency is consistent with that found in a subtropical forest, whereas other seasonally varied ecosystems had the opposite relations (Zhu et al., 2014). Zhu et al. attributed the positive correlations between WUE and air temperature that they observed to the seasonal variation of LAI–canopy structure. That is, the larger the leaf area that developed, the smaller the evaporation from the soil surface. However, the subtropical forest had no seasonal LAI variation (LAI <= 4) and primary production there varied little seasonally; thus, WUE was decreased by increasing transpiration demand as air temperature rose there. We might apply to our site (LAI was generally larger than 4) the same explanation as was applied to the subtropical forest. There was a peak LUE value with daytime average $T_c$ 15-20 °C in each experimental year, which tended to increase with elapsed year after the clear-cutting (Fig. 6b). We attributed this tendency to reflect the temperature–photosynthesis

### Table 1. Coefficients of the regression line between daytime average water use efficiency (WUE) and vapor pressure deficit (D$_v$) and between daytime average light use efficiency (LUE) and D$_v$. WUE is expressed as WUE = $a_0 \exp(b_0 D_v)$, and LUE as LUE = $c_0 + d_0$. 

| D$_v$–WUE | D$_v$–LUE |
|------------|-----------|
| $a_0$      | $b_0$     | $R^2$     | $c_0$ | $d_0$ | $R^2$     |
| 2002       | 46.06     | -0.797    | 0.65  | -9.43 | 27.57    | 0.89      |
| 2003       | 16.90     | -0.324    | 0.45  | -2.71 | 12.58    | 0.63      |
| 2004       | 34.90     | -0.595    | 0.88  | -3.19 | 14.61    | 0.74      |
| 2005       | 30.08     | -0.303    | 0.78  | -2.56 | 20.04    | 0.78      |
| 2006       | 40.55     | -0.396    | 0.68  | -1.80 | 19.03    | 0.56      |
| 2007       | 39.21     | -0.338    | 0.60  | -4.20 | 22.14    | 0.56      |
| 2008       | 48.28     | -0.577    | 0.84  | -4.54 | 23.79    | 0.79      |
| 2009       | 42.15     | -0.508    | 0.80  | -4.77 | 23.48    | 0.82      |
| 2010       | 26.08     | -0.252    | 0.69  | -4.67 | 26.95    | 0.89      |

### Table 2. Coefficients of the regression line between daytime average water use efficiency (WUE) and photosynthetically active radiation (PAR) and between daytime average light use efficiency (LUE) and PAR. WUE is expressed as WUE = $a_v \exp(-b_v \text{PAR})$, and LUE as LUE = $c_v \text{PAR} + d_v$. 

| PAR–WUE | PAR–LUE |
|---------|---------|
| $a_v$  | $b_v$  | $R^2$ | $c_v$ | $d_v$ | $R^2$ |
| 2002    | 74.33  | -0.00132 | 0.84  | -0.0175 | 35.15 | 0.91  |
| 2003    | 28.55  | -0.00133 | 0.78  | -0.0123 | 18.12 | 0.93  |
| 2004    | 49.89  | -0.00157 | 0.96  | -0.0097 | 17.88 | 0.89  |
| 2005    | 47.76  | -0.00101 | 0.88  | -0.0128 | 27.37 | 0.87  |
| 2006    | 75.69  | -0.00145 | 0.87  | -0.0137 | 28.19 | 0.87  |
| 2007    | 75.55  | -0.00113 | 0.88  | -0.0141 | 31.33 | 0.92  |
| 2008    | 62.28  | -0.00124 | 0.90  | -0.0150 | 30.71 | 0.93  |
| 2009    | 65.97  | -0.00135 | 0.94  | -0.0145 | 30.01 | 0.97  |
| 2010    | 35.03  | -0.00078 | 0.88  | -0.0180 | 36.45 | 0.89  |

Fig. 5. The relationship between seasonal maximum leaf area index ($\text{LAI}_\text{max}$) and the slope of the regression line between light use efficiency (LUE) and photosynthetically active radiation (PAR) ($c_P$ in Table 2), and (b) $\text{LAI}_\text{max}$ and the y-intercept of the line ($d_v$ in Table 2). The determination coefficients ($R^2$) are (a) 0.77 and (b) 0.69.
curve in this ecosystem, and the optimum temperature would increase in accordance with the development of the vegetation. Our peak values of air temperature on the LUE–temperature curve were a little higher than those observed in a mixed coniferous forest in Sweden (Lagergren et al., 2005), where the values were approximately 14–16°C.

Fig. 6. The relationship between (a) daytime average water use efficiency (WUE) and air temperature (T_a) and (b) daytime average light use efficiency (LUE) and T_a, where T_a was bin-averaged by every 2°C. The gray bars in these figures represent standard deviation.

Fig. 7. The relationship between (a) daytime average water use efficiency (WUE) and soil water content (SWC), and (b) daytime average light use efficiency (LUE) and SWC, where SWC was bin-averaged by every 2%. The gray bars in these figures represent standard deviation.
There was no consistent effect of SWC on the variation of WUE (Fig. 7a). In terms of the relationship between LUE and SWC, there were 3 increasing trend years (2002, 2003, and 2009) and 5 decreasing trend years (2004–2007 and 2010). Daytime average SWC ranged between 30 % and 60 % during each experimental year, indicating there had been no drought. The relatively narrow range of SWC at this site might not significantly affect the variation of LUE and WUE (Fig. 7).

Except for the years 2003 and 2010, WUE tended to decrease with increasing $G_s$, whereas there was a weak increasing tendency between LUE and $G_s$ during every experimental year (Fig. 8). We attribute the increase of LUE with $G_s$ on WUE means that the stomatal control was more effective on transpiration than on photosynthesis; this result is consistent with those obtained in previous leaf-scale studies (Farquhar and Sharkey, 1982).

4. Summary and conclusion

We evaluated inter-annual and seasonal variation of WUE and LUE over 9 years in a cool-temperate forest under a series of forestry management protocols of clear-cutting and planting. We elucidated effects of these protocols on the variation in or the relationship with environmental and vegetation factors. WUE and LUE largely decreased after clear-cutting, in accordance with the decreased GPP. A recovery trend of GPP and ET was observed after 2005, and by 2010 their values had returned to almost the same level as those before clear-cutting. WUE and LUE were negatively corresponded with PAR and $D_0$ in their seasonal variation, and LUE increased with increasing LAI in accordance with vegetation recovery. Other environmental and vegetation factors did not explain the changes in WUE and LUE. Accordingly, we can explain the clear-cutting effect on LUE by the change in the LAI. Vegetation composition (developed forest or young tree seedlings with dense undergrowth) had little effect on the magnitude and variation of LUE, while the change in LAI scarcely affected WUE because of WUE’s stronger sensitivity to the atmospheric water deficit than to vegetation structure. This finding can simplify the model application to estimate ecosystem GPP only by using LAI for the vegetation information. ε models use only remotely sensed data, such as PAR (Frouin and Pinker, 1995) and LAI (le Maire et al., 2012). Such remotely sensed data can derive not only PAR (Frouin and Pinker, 1995) but also LAI (le Maire et al., 2012). Thus, when regional or vegetation-specific WUE and LUE are known, the regional evapotranspiration as well as GPP for similar types of ecosystems could be estimated from satellite data.

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