Characterization of Canopy Photosynthetic CO₂ Flux and Leaf Stomatal Conductance Responses of Potato Crop to Changing Field Meteorological Conditions in Hokkaido

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Abstract

This study characterizes the response of canopy CO₂ flux (F_{CO₂}) and leaf stomatal conductance (gs) of potato fields in the Tokachi plain in Hokkaido to changing meteorological factors, e.g. air temperature and vapor pressure deficit (VPD_a). Measurements were made of F_{CO₂} and meteorological conditions in August 1998. Also, upper crown sunlit leaf stomatal conductance response to air temperature and vapor pressure deficit (VPD_c) inside the cuvette of a porometer were measured simultaneously on a number of days to determine their effects on gs. Results showed that at moderate summer temperatures in Hokkaido and free soil water stress, VPD_a was the more significant factor affecting the depression in F_{CO₂} in the potato crop. The depression is characterized by the difference of F_{CO₂} from a curve tracing the maximum F_{CO₂} response to light. A similar VPD_c effect was also observed in gs. Above an optimum temperature of 25°C, stomatal closure and high depressions in photosynthetic CO₂ exchange occurred even at low vapor pressure deficit. This fact implies a decrease in photosynthetic CO₂ fixation and crop growth in cool temperate-climate regions under further global climate warming.

Key words: Canopy CO₂ flux, Stomatal conductance, Temperature, Vapor pressure deficit.

1. Introduction

In view of the impacts of future climatic variations on agricultural production in cool temperate regions, there is an increasing demand to maintain those systems sustainable through a continuous assessment of changes in plant growth and productivity imposed by warming (Parry and Carter, 1988). In this respect, several authors have pointed out the importance of canopy CO₂ flux as a significant tool for the quantitative assessment of the impact of environmental changes upon biological processes (Garcia et al., 1990) and for the management of plant growth and agriculture at a regional scale (Hideshima et al., 1997). However, limited basic information exists detailing the characteristic contribution of climatic factors, in particular temperature and vapor pressure deficit, to the canopy CO₂ flux response and growth patterns of major crops cultivated in Hokkaido. In developing warming scenarios for Hokkaido, Yoshino et al. (1988) have adopted temperature as the key climatic limiting factor to rice
growth in that area. If this hypothesis can be proved experimentally with regard to locally cultivated crop species that differ in their climatic requirements, then we might have a general and reliable tool for monitoring the changes of canopy CO₂ flux and crop growth at a local scale in response to climatic variation.

In this study canopy CO₂ flux (F_{CO₂}) and leaf stomatal conductance (gs) of a field grown potato crop were examined to provide insight into the likely response of vegetation growth to changes in the major field climatic factors, particularly leaf-to-air vapor pressure deficit and air temperature. This finding would characterize the crop relative photosynthetic response to both factors for a review of their parameterization in micrometeorologically-based canopy photosynthesis models under a changing climate.

2. Methods

2.1 Field description and period of measurement

This study was conducted on a private farmer's field (1.8 ha) located in a large cropping area in Nakasatsunai village in Tokachi plain in Hokkaido (42°50’N and 143°10’E). Measurements were carried out in the field from 1 until 23 August. The field was surrounded by similar potato cultivation at similar growth stage.

Potatoes (Solanum tuberosum, cv. Konafubuki) were sown on 28 April at 33 cm spacing within each row and 72 cm between rows. Fertilizers were applied one week prior to cultivation and pest control was carried out almost weekly starting in late June.

Throughout the measurement period, frequent ample rainfall characteristic of that northern temperate location maintained the soil water content near field capacity. The potato crop was in full stage of growth and the vegetation height and vegetation coverage were 50 cm and 95% respectively. Prior to measurements, the leaf area index was estimated at about 5 using the relation developed by the authors between coverage and leaf area index.

2.2 Micrometeorological and canopy CO₂ flux measurements

These were made for 23 consecutive days with a Bowen ratio measurement system with dual psychrometer heads (Aoki et al., 1996). The heights of the upper and lower psychrometers above ground level were 2.2 m and 0.8 m respectively. The system was installed near the center of the potato field. The minimum fetch of this potato field was about 100 m. Since this field was surrounded by similar potato cultivation of the same crop height, the fetch was considered enough for measurement by Bowen ratio technique.

2.2.1 Description of sensors and measured variables

Canopy CO₂ flux and micrometeorological data were collected continuously for 23 consecutive days. Table 1 summarizes the measured variables and their symbols. These included ambient CO₂ concentration measured with a CO₂ gas analyzer (LI-COR Inc., model LI-6262). Gas samples were collected from two heights of 0.3 m and 1.7 m above vegetation canopy, the same heights at which the psychrometers were placed, and were first supplied to an air sampling system (METEO electric, model Met-SCI) containing a micro-processor that commands an mechanical valve alternating a 3 min switching rotation of intake gas between the upper and lower gas samples. Sample gas was then forced with the same circuit into the CO₂ gas analyzer at a rate of 1 litre/
An air pump (REICI, model APN-057R-D2) was used to draw air samples at those two elevations through funnels extended to Teflon tubes (PFA tubes of 6 mm diameter) and connected to the air sampling system and then to the LI-COR analyzer. The CO₂ concentration gradients were automatically measured by the air sampling system and averaged into 3 min data. The LI-6262 was automatically calibrated every 24 hours using a zero reference gas for the Zero CO₂, and a standard gas of known CO₂ concentration for the span.

Air temperature and relative humidity were obtained from the dry- and wet-bulb temperatures of the psychrometer at 1.7 m above canopy. Wind speed above the canopy was measured with an anemometer mounted at the top of the 4 m pole (YOUNG, model 05103-16B). Solar radiation was observed with a solarimeter (KIP & ZONEN, model PMC-3) leveled at 1.5 m above ground. Soil water moisture was determined from the average of three readings from three tensiometers (KONA system, model KDC-S5) buried at 15 cm depth at three different locations near the pole. Soil temperature was the average of two values from two thermistors (KURAMO, model KVC-36) installed at 1 cm and 15 cm.

In addition soil heat flux and net radiation were measured to compute FCO₂. Net radiation (RN; Wm⁻²) was determined with a net radiometer (EKO, model MF-40) mounted at 1 m above vegetation canopy. Soil heat flux (G; Wm⁻²) was the average reading of three heat flux plates (EKO, model MF-81) buried at 1 cm in the soil.

Soil respiration was measured with a soil respiration chamber for a limited duration and was found to be almost constantly within 5% of FCO₂ in the daytime under dense canopy. Although soil respiration is an essential factor to compute net CO₂ uptake, in this study we assumed that such a small and stable soil respiration rate has a negligible effect on the behavior of canopy CO₂ flux (Sale, 1974).

Data from the above sensors were scanned every 1 min, averaged every 10 min and stored in a data logger (METEO electric, model MET LD-30). All data were then reduced into 30 min average values to maintain consistency with the micrometeorological literature (Monteith, 1973). Only daytime measurements from 8:00 h to 15:00 h JST were selected for this study. These measurements were checked on a daily basis to detect any failure of sensors that often caused incomplete data that could not be considered for analysis.

### 2.2.2 Method of canopy CO₂ flux determination

In this study canopy FCO₂, expressed as grams of CO₂ per square meter of ground area per hour, was determined by multiplying a transport coefficient (D) with the gradient of the ambient CO₂ concentration (ΔC) measured above vegetation canopy (Eq. 1).

\[ F_{CO_2} = D \times \Delta C \]

The transport coefficient (D) is determined by the energy balance method as shown by Monteith (1973) with the following equation:

\[ D = \frac{R_n - G}{\rho_s \times \lambda \times \Delta e \cdot 0.622 + C_p \times \rho_e \times \Delta t} \]

Where \( \rho_s \) (kg m⁻³) is the air density, \( \lambda \) (J kg⁻¹) is the heat of vaporization of water, and \( P \) (Pa) is the atmospheric pressure, \( C_p \) (J kg⁻¹ K⁻¹) is the specific heat of air at constant pressure and \( \Delta e \) (Pa) and \( \Delta t \) (°K) are respectively the air vapor pressure difference and the temperature difference between the psychrometers at the two elevations above canopy.

Finally FCO₂ is obtained by substituting the expression of D in Eq. (2) into Eq. (1).

### 2.3 Measurements of leaf stomatal conductance

Simultaneously, a steady state porometer (LI-COR, Inc., LI-1600) was used to measure individual leaf stomatal conductance (gs; cm s⁻¹). Porometer air temperature (\( T_c \); °C) and porometer leaf-to-air vapor pressure deficit (VPDc; hPa) were measured together with the stomatal conductance of the abaxial leaf surface on 6 separate days between Aug. 1 and Aug. 23. Measurements were taken only during fine weather at intervals varying between 3 and 5 min with a standby period of 10–15 min for every round of 2 hours of measurements starting from around 8:00 h to around 15:00 h. On many days, due to overnight rain, measurements in the morning were started 2 to 3 hours after 8:00 h after the canopy had become completely dry. Mature and fully expanded sun leaves representing different orientations in the upper canopy of randomly selected plants were measured. In this paper stomatal conductance of water vapor is used for analysis.

### 3. Results

#### 3.1 Canopy photosynthetic CO₂ flux

Table 1 shows the means and standard deviations of the measured environmental conditions and calcu-
lated $F_{CO_2}$ for the whole study period. Canopy $F_{CO_2}$ and most of the climatic-environmental variables varied considerably. With regard to soil moisture, the soil was wet due to heavy rainfall on many separate days during the period of measurements. In general, drought in this region does not usually occur in August due to sufficient amount of rainfall. This would suggest that soil water stress by soil moisture shortage might not have occurred during this study. The mean value of air temperature closely coincided with the July–August mean temperature (20.6°C) of the baseline climate in Hokkaido (1951–1980) as provided by Yoshino et al. (1988). Ambient $CO_2$ was the least variable.

The response of the canopy $F_{CO_2}$ to various factors was based on the approach proposed by Jones (1992) of a hypothetical boundary-line relationship between $F_{CO_2}$ and solar radiation ($I$) as shown in Fig. 1. In this figure the widely scattered data are field measured $F_{CO_2}$. The maximum values of $F_{CO_2}$ observed within the interval of 25 Wm$^{-2}$ to 800 Wm$^{-2}$ of solar radiation were selected. These selected values were assumed to represent the maximum response of $F_{CO_2}$ under optimal field conditions and were fitted with a solid curve that traces the potential maximum curve of $F_{CO_2}$ response to light ($Max F_{CO_2}$). That curve was calculated from our data with a simplified expression of the hyperbolic rectangular formula of net photosynthetic response (Thornley and Johnson, 1990) having the form of:

$$ F_{CO_2} = \frac{I}{\sigma + \omega I} $$

(3)

with $I$ is solar radiation, $\sigma$ is the reciprocal of photosynthetic efficiency and $\omega$ is the reciprocal of the maximum photosynthetic rates at saturated light intensities.

The resulting depression from this maximum photosynthetic response ($\Delta F_{CO_2}$) in Fig. 1 was assumed to be caused by the environmental factors shown in Table 1. Further analysis of $\Delta F_{CO_2}$ against meteorological/soil variables revealed major influences of $VPD_a$ and $T_a$ (Fig. 2 (a) and Fig. 2 (b) respectively). Throughout the whole measurements, however the interaction between $VPD_a$ and $T_a$ was not very strong ($r^2=0.53$). In order to reveal the more explanatory variable and quantify its main influence on $\Delta F_{CO_2}$ the following analysis was conducted. The response of $\Delta F_{CO_2}$ to changes in $T_a$ was analyzed in each of 5 groups of $VPD_a$ (Fig. 3 (a)). Secondly, the relationship between $\Delta F_{CO_2}$ and $VPD_a$ was sorted into 6 groups of increasing temperature (Fig. 3 (b)). Quantitative study of the effect of either $T_a$ or $VPD_a$ on $\Delta F_{CO_2}$ in both figures was based on the analysis of the linear regressions fitted to each group of data and the comparison of their straight-line slopes.

Fig. 1. Light response of canopy $F_{CO_2}$ of a potato crop for the whole measurement period. The scattered dots are the observed $F_{CO_2}$ in the field and the solid curve is the $Max F_{CO_2}$ calculated by the hyperbolic rectangular photosynthesis light model.

$$ \Delta F_{CO_2} = Max F_{CO_2} - F_{CO_2} $$

Fig. 2. Relationship of $\Delta F_{CO_2}$ to (a) air temperature ($T_a$) and (b) air vapor pressure deficit ($VPD_a$).
In Fig. 3 (a), $\Delta F_{\text{CO}_2}$ appeared to increase in response to $T_s$ and also to increasing $VPD_a$. In Fig. 3 (b), the increase of $\Delta F_{\text{CO}_2}$ in response to $VPD_a$ was steady, almost independent of changing temperature. The slopes relating $\Delta F_{\text{CO}_2}$ to $VPD_a$ showed a significant effect by $VPD_a$ for all temperature ranges (Table 2). At the highest range of temperature e.g. 24–27°C (Group F in Fig. 3 (b)), the sensitivity of $\Delta F_{\text{CO}_2}$ to $VPD_a$ seems to reach a standby level with relatively high depressions occurring at a wide $VPD_a$ range covering low as well as high values.

3.2 Stomatal Conductance

Although the total scatter of $gs$ response to cuvette $T_c$ in Fig. 4 (a) shows no significant trend, the $VPD_c$ response in Fig. 4 (b) showed a commonly observed decline in stomatal conductance (Ball et al., 1987; Turner, 1991; Bunce, 2000a). Stomatal conductance appeared to over-range, especially at the lowest $VPD_c$ and optimal temperature values. Since the interaction between $VPD_c$ and $T_c$ was not strong ($r^2=0.45$), the dependence of stomatal behavior on these two factors was investigated following the same approach described earlier for $\Delta F_{\text{CO}_2}$ by analyzing the slopes of linear relationships fitted to $VPD_c$ groups in Fig. 4 (a) and $T_c$ groups in Fig. 4 (b) respectively.

In Fig. 4 (a), the $gs$ response to temperature seemed to decline mainly with increased $VPD_c$ ranges.

In Fig. 4 (b), the slopes relating $gs$ to $VPD_c$ at every temperature range showed a high sensitivity of $gs$ to $VPD_c$. This sensitivity decreased gradually with the increase in temperature ranges as can be deduced from the changes in the values of the slope $VPD_c$ in Table 3. At the highest temperature range e.g. 26–28.5°C (Group E in Fig. 4 (b)), the slope of regression to $VPD_c$ showed the least sensitivity of $gs$ response to this factor as it occurred over a wide

![Fig. 3. Canopy $\Delta F_{\text{CO}_2}$ in response to (a) $T_s$ and (b) $VPD_a$.](image)

(a) A: $0 \leq VPD_a < 2$ hPa,
B: $2 \leq VPD_a < 5$ hPa,
C: $5 \leq VPD_a < 8$ hPa,
D: $8 \leq VPD_a < 11$ hPa,
E: $11 \leq VPD_a \leq 18.3$ hPa
(b) A: $14 \leq T_s < 16^\circ C$, B: $16 \leq T_s < 18^\circ C$,
C: $18 \leq T_s < 20^\circ C$, D: $20 \leq T_s < 22^\circ C$,
E: $22 \leq T_s < 24^\circ C$, F: $24 \leq T_s \leq 27.1^\circ C$

Slopes represent the linear regression fits analyzed in Table 2.

![Table 2. Linear regression analysis of $\Delta F_{\text{CO}_2}$ versus $T_s$ and $VPD_a$ respectively.](image)

<table>
<thead>
<tr>
<th>Group labels</th>
<th>Intercept</th>
<th>Slope $T_s$</th>
<th>$s$</th>
<th>$r^2$</th>
<th>$n$</th>
<th>Intercept</th>
<th>Slope $VPD_a$</th>
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<td>$1.07$</td>
<td>$0.02$</td>
<td>119</td>
<td>$1.03$</td>
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<td>$0.65$</td>
<td>$0.2$</td>
<td>88</td>
</tr>
<tr>
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<td>$-0.99$</td>
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<td>$1.13$</td>
<td>$0.08$</td>
<td>64</td>
<td>$1.23$</td>
<td>$0.21^1$</td>
<td>$0.97$</td>
<td>$0.15$</td>
<td>91</td>
</tr>
<tr>
<td>D</td>
<td>$-2.22$</td>
<td>$0.27^1$</td>
<td>$1.11$</td>
<td>$0.15$</td>
<td>46</td>
<td>$1.17$</td>
<td>$0.25^1$</td>
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<td>E</td>
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<td>20</td>
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<tr>
<td>F</td>
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<td>$0.12^1$</td>
<td>$0.89$</td>
<td>$0.23$</td>
<td>34</td>
<td></td>
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</table>

$n =$ number of observations ; $r^2 =$ coefficient of determination ; $s =$ standard error of the estimate.

* Letters denote the ranges of $VPD_a$ and $T_s$ groups in Fig. 3 (a) and Fig. 3 (b) respectively.

$^1$ Effect of the independent variable on $\Delta F_{\text{CO}_2}$ at the 5% significant level tested by ANOVA.
interval of VPDc values.

4. Discussion

Measured environmental conditions on average were normal for potato growth. Neither strong water stress nor large variation in ambient CO2 was apparent in the field due to the frequent rainfall and the absence of any CO2 polluting source during daylight measurements. Solar radiation was highly variable, mostly due to variable cloud cover. The measured FCO2 in potato showed a wide variation and large depression in response to solar radiation (Fig. 1), though a hyperbolic rectangular response has been reported for leaf and canopy photosynthesis in potato species (Sale, 1974; Ku et al., 1977).

The resulting depression in FCO2 in potato was more sensitive to the variation of VPDa than to the moderate air temperature values. A similar finding was also observed in gs in response to VPDc at normal Tc. Given the wet field conditions during measurements, this strong response of vapor pressure deficit does not seem to be the result of a shortage in water supply to meet increased evaporative demand. The lower sensitivity to temperature at less than the optimum value (25°C) in both cases, e.g. ∆FCO2 and the decline in gs may agree with the findings of Ku et al. (1977), Ball et al. (1987) and Bunce (2000 a). At similar moderate temperature values, Baldocchi et al. (1981) and Sale (1974) reported almost no temperature effect on FCO2 in an alfalfa field and canopy net photosynthesis of potato species respectively.

Above optimum temperature, the lowered sensitivity in ∆FCO2 and the decline in gs were observed at a wide range of vapor pressure deficit covering low and high values. This decreased sensitivity of FCO2 and gs to vapor pressure deficit at temperatures exceeding the optimum value of 25°C seems to agree with the work by Ball et al. (1987) and Bunce (2000 a). This present finding however, does not necessarily suggest that a more effective temperature response will take place under very hot conditions, since previous experimentation has shown the capacity of plants to acclimate to extreme temperatures (Bunce, 2000 b).

Fig. 4. Leaf gs response to (a) Tc and (b) VPDc.
(a) A: 5 ≤ VPDc < 8 hPa,
B: 8 ≤ VPDc < 11 hPa,
C: 11 ≤ VPDc < 14 hPa,
D: 14 ≤ VPDc < 17 hPa,
E: 17 ≤ VPDc ≤ 26 hPa
(b) A: 18 ≤ Tc < 20°C, B: 20 ≤ Tc < 22°C,
C: 22 ≤ Tc < 24°C, D: 24 ≤ Tc < 26°C,
E: 26 ≤ Tc ≤ 28.5°C
Slopes represent the linear regression fits analyzed in Table 3.

Table 3. Linear regression analysis of gs to Tc and VPDc respectively.

<table>
<thead>
<tr>
<th>Group labels</th>
<th>Intercept</th>
<th>Slope Tc</th>
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<th>r^2</th>
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<th>Intercept</th>
<th>Slope VPDc</th>
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<td>0.55</td>
<td>23</td>
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<tr>
<td>B</td>
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<td>0.07^1</td>
<td>0.41</td>
<td>0.11</td>
<td>57</td>
<td>3.8</td>
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<td>0.34</td>
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<td>56</td>
</tr>
<tr>
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<td>0.32</td>
<td>0.46</td>
<td>156</td>
<td>3.45</td>
<td>-0.22^1</td>
<td>0.41</td>
<td>0.71</td>
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<tr>
<td>D</td>
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<td>0.03^1</td>
<td>0.21</td>
<td>0.05</td>
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<td>3.1</td>
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<td>0.13</td>
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<td>-0.1^1</td>
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<td>0.44</td>
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n = number of observations; r^2 = coefficient of determination; s = standard error of the estimate.

*Letters denote the ranges of VPDc and Tc groups in Fig. 4 (a) and Fig. 4 (b) respectively.

^1 Effect of the independent variable on ∆FCO2 at the 5% significant level tested by ANOVA.
This specific question may require further investigations of vapor pressure deficit and temperature responses under field conditions during years of extreme temperature fluctuations.

5. Conclusions

At moderate summer temperatures in Hokkaido and non-limiting soil moisture, $VPDa$ was the more significant factor affecting the depression in $F_{CO_2}$ in potato. This depression was defined from the difference of $F_{CO_2}$ from a curve tracing the maximum $F_{CO_2}$ response to solar radiation. A similar $VPDe$ effect was observed to cause stomatal closure at normal $T_c$. Above the optimum temperature of 25°C, stomatal closure and high depressions in photosynthetic $CO_2$ exchange occurred even at low vapor pressure deficit. This finding suggests further consequences in crop growth and productivity under global climate warming.

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References


北海道のジャガイモ畑における群落 CO₂フラックスおよび葉の
気孔コンダクタンスに及ぼす気象条件の影響特性解析

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要 約

この研究は、北海道十勝平野のジャガイモ畑における
群落光合成に伴う CO₂フラックス (FCO₂) および葉の気
孔コンダクタンス (gs) に及ぼす気温や飽和などの気象
条件の影響を調べ、その反応特性を解析したものであ
る。測定は、現地の畑において、1998年8月に、CO₂フ
ラックス (FCO₂) および気象条件について行った。また、
その期間中の数日間、よく日の当たる群落上部の葉の気
孔コンダクタンスをポロメータで同時測定し、ポロメー
タ内の気温と飽和 (VPDc) に及ぼす影響も調べた。その
データを解析したところ、土壤水分が十分であったにも
かかわらず、FCO₂の低下は主に野外の飽和 (VPDa) の
影響であることが分かった。FCO₂の低下特性は、光一