

양파 광합성 예측을 위한 잎의 기체교환모형 모수 추정

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Leaf Gas-exchange Model Parameterization and Simulation for Estimating Photosynthesis in Onion

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ABSTRACT

Process-based model (PBM), based on the interactions between endogenous physiological processes and many environmental factors, can be a powerful tool for estimating crop growth and productivity. Carbon acquisition and biomass accumulation are the main components in PBM, so it has become important to understand and integrate gas exchange process in crop model. This study aimed to assess the applicability of FvCB model (a leaf model of C_3 photosynthesis proposed by Farquhar, von Caemmerer, and Berry (1980)) in onion (*Allium cepa* L.). For parameterization, two early-maturing onion cultivars, 'Singsingball' and 'Thunderball', grown in a temperature gradient plastic film house, were used in measuring leaf net CO_2 assimilation rate (A), and then, parameter estimation was carried out for four parameters including V_{cmax} (maximum rate of carboxylation), J_{max} (maximum rate of electron transport), TPU (rate of triose phosphate utilization), and R_d (Dark respiration rate). The gas-exchange model calibrated in this research is expected to be able to explain the photosynthetic responses of onion under various environmental conditions ($R^2=0.95^{***}$).

Key words: Crop model, Carbon assimilation, Physiological process, *Allium cepa*

I. Introduction

Onion is one of the five major vegetables as essential ingredient for Kimchi. Since onion is grown under relatively low temperature in open field, it is susceptible to temperature rise caused by climate change in winter. In order to reduce the uncertainty in food production under changing climate, many

efforts have been made to accurately predict the crop production by linking the physiological processes and the accumulation of biomass in plants. However, the empirical model based on the regression method has a problem that the predictable range is limited to the environmental conditions and varieties used in the modeling (Simane *et al.*, 1994). On the other hand, the process-based model, which belongs to the



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mechanistic (explanatory) model, enables accurate yield prediction by simulating the interaction between plants and environmental conditions based on physiological metabolic processes (Buck-Sorlin, 2013).

Photosynthesis is an important physiological process that determines crop growth and yield by introducing fixed carbon and energy into agricultural ecosystems (Jones, 2014). The gas-exchange model provides a basic framework for predicting the net carbon assimilation rate under field conditions through leaf photosynthesis simulation. Leaf photosynthesis model proposed by Farquhar *et al.* (1980) is based on the biochemical mechanism in which the rate of photosynthesis is determined by Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase)-mediated carboxylation, RuBP regeneration controlled by electron transport, and the availability of triose phosphate (Sharkey *et al.*, 2007). In the model, the initial slope of the CO₂ response curve is related to the *in vitro* Rubisco activity of C₃ plants, and the CO₂ saturation rate in the *A-Ci* curve is related to the *in vitro* measurement of electron transport rate (Bernacchi *et al.*, 2003). The Farquhar model was adopted for predicting leaf-level photosynthesis in the sun/shade model of canopy photosynthesis (De Pury and Farquhar, 1997). Meanwhile, the sun/shade model of canopy photosynthesis, based on the dynamic differences in photosynthesis of sunlit and shaded leaves, effectively overcame the problem of big leaf and multi-layer models. The predictive accuracy and simplicity of the sun/shade model provides the basis for incorporating leaf-level photosynthesis into higher processes, crop growth model.

So far, only ALCEPAS model has been reported for onion, which is based on SUCROS87 simulating the potential growth of crops depending on the radiation use efficiency (de Visser, 1994). However, this model has the drawback of simulating crop growth only when weeds, pests, diseases, and soil conditions do not limit growth, and there are sufficient water and nutrients. In this study, parameter estimation and calibration of the model were carried

out to expand the gas-exchange model, a key process for developing comprehensive process-based model reflecting crop growth and productivity, into onion.

II. Materials and Methods

2.1. Plant material and gas exchange measurements

The field experiment was conducted during the growing season in a temperature gradient plastic film house at Research Institute of Climate Change and Agriculture in Jeju, South Korea (33°28'06.7"N, 126°31'03.5"E). Seedlings of early-maturing onion cv. 'Singsingball' and 'Thunderball' were transplanted at a density of 25 plants m⁻² on 31 October and 12 November in 2019, respectively (about 45~55 days after sowing). The temperature gradient (about + 6°C from outside temperatures) was maintained along the tunnel from transplanting to harvest, and the average daily irradiance was 607.7 μmol m⁻² s⁻¹. Fully-expanded healthy leaves were used in photosynthesis measurement by an open gas-exchange system with a 6 cm² leaf cuvette (LI-6400XT, LI-COR, Lincoln, USA) during bulb enlargement period from April to May in 2020. Flow rate 500 μmol s⁻¹, block temperature 25°C, photosynthetically active radiation (PAR) 1,500 μmol m⁻² s⁻¹, relative humidity (RH) 50~60%, and reference CO₂ concentration of 50, 100, 200, 400, 600, 800, 1,100, 1,400, 1,700, and 2,000 μmol mol⁻¹ were used for fitting *A-Ci* curve.

2.2. Parameterization and calibration of the model

V_{cmax} , J_{max} , TPU , and R_d , the main parameters of leaf gas-exchange model, were determined, based on FvCB model (a leaf model of C₃ photosynthesis proposed by Farquhar *et al.* (1980)) and photosynthesis measurement data obtained from temperature gradient tunnel. Curve fitting utility model (Sharkey *et al.*, 2007) was used for estimating photosynthetic CO₂ response curves. Points below 200 μmol mol⁻¹ were assigned as Rubisco-limited, and points above 300 μmol mol⁻¹ as RuBP-regeneration limited. Points between 200 and 300 μmol mol⁻¹ were

Table 1. The constant values used for parameter estimation process of leaf gas-exchange model in onion

Parameter [†]	at 25°C	c (dimensionless)	ΔH_a (kJ mol ⁻¹)	Reference
V_{cmax} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.00	26.35	65.33	<i>Bernacchi et al. (2001)</i>
J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.00	17.57	43.55	<i>Bernacchi et al. (2003)</i>
TPU ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.00	21.46	53.10	<i>Sharkey et al. (2007)</i>
R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.00	18.72	46.39	<i>Bernacchi et al. (2001)</i>
K_c ($\mu\text{mol mol}^{-1}$)	404.90	38.05	79.43	"
K_o (mmol mol^{-1})	278.40	20.30	36.38	"
Γ^* ($\mu\text{mol mol}^{-1}$)	42.80	19.02	37.83	"

[†] V_{cmax} : maximum rate of carboxylation by Rubisco, J_{max} : maximum rate of RUBP regeneration by electron transport, TPU : rate of triose phosphate utilization, R_d : Dark (or day) respiration rate, K_c : Michaelis-Menten constant of Rubisco for CO₂, K_o : Michaelis-Menten constant of Rubisco for O₂, Γ^* : photorespiratory compensation point.

Table 2. Parameters estimated for application of leaf gas-exchange model in onion

Parameter	V_{cmax}	J_{max}	TPU	R_d
Mean \pm S.D.	118 \pm 21	217 \pm 26	17.3 \pm 2.9	4.0 \pm 1.6

[†]Normalized to unity at 25°C based on *Bernacchi et al. (2003)*

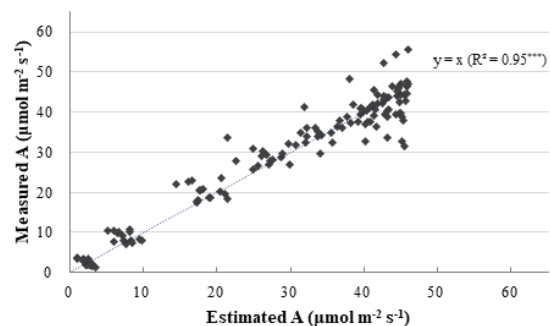
assigned as 0. The last point at the top of the curve that are constant or declining with CO₂ concentration was assigned as TPU limited. Finally, the output values minimizing the sum of squares were derived from the model.

Γ^* , CO₂ compensation point in the absence of dark respiration, was fixed to 42.8 $\mu\text{mol mol}^{-1}$ (*Bernacchi et al., 2001*), and θ , a constant related with the curvature of A - C_i curve, was calibrated to 0.9857. Scaling constants, activation energy and Michaelis-Menten constants for CO₂/O₂ were adopted from *Bernacchi et al. (2001)*, *Bernacchi et al. (2003)* and *Sharkey et al. (2007)*, and described in Table 1.

III. Results and Discussion

3.1. Gas-exchange model for estimating leaf photosynthesis in onion

Predicting the rate of photosynthesis in onion leaves is a key process in process-based modeling. The main parameters of the gas-exchange model, V_{cmax} , J_{max} , TPU , and R_d , were estimated using the photosynthesis measurements of onion leaves grown

**Fig. 1.** Parameterization of leaf gas-exchange model for onion leaves. Measured and estimated net CO₂ assimilation rates (A) were compared.

in a temperature gradient house, and described in Table 2. The relationship between the observed (measured) data and estimated values by gas-exchange model was described in Fig. 1. The gas-exchange model was proved to provide an accurate prediction on CO₂ response curve with about 95% confidence ($R^2=0.95^{***}$) when θ (theta) is calibrated to 0.9857. This means that the leaf gas-exchange model can be applied to various crops through parameter estimation and modification. There

are some reports on the application of the gas-exchange model to rose (Kim and Lieth, 2003) and garlic (Kim *et al.*, 2013). These previous researches showed that the gas-exchange model based on underlying biochemical mechanisms can give accurate prediction on actual photosynthesis, and can be widely accepted to various crops for mechanistic modeling.

3.2. Model simulation for evaluating interactions with environmental factors

The results of leaf gas-exchange model simulation on CO₂, light, and temperature response curves were

described in Fig. 2. The estimated A (net CO₂ assimilation rate) at saturating light (PPFD = 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in 400 $\mu\text{mol mol}^{-1}$ CO₂ and air temperature near 25°C was 27.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2A). Photosynthetic CO₂ response curve showed that A_{sat} (light-saturated photosynthesis) reached above 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with saturating CO₂ concentration in moderate leaf temperatures ($\approx 25^\circ\text{C}$). Elevated CO₂ concentration stimulated A_{sat} in C₃ plants grown under free-air CO₂ enrichment (FACE) by an average of 31%, although nitrogen supply and sink capacity modulated the response of photosynthesis to elevated CO₂ concentration through their impact on the

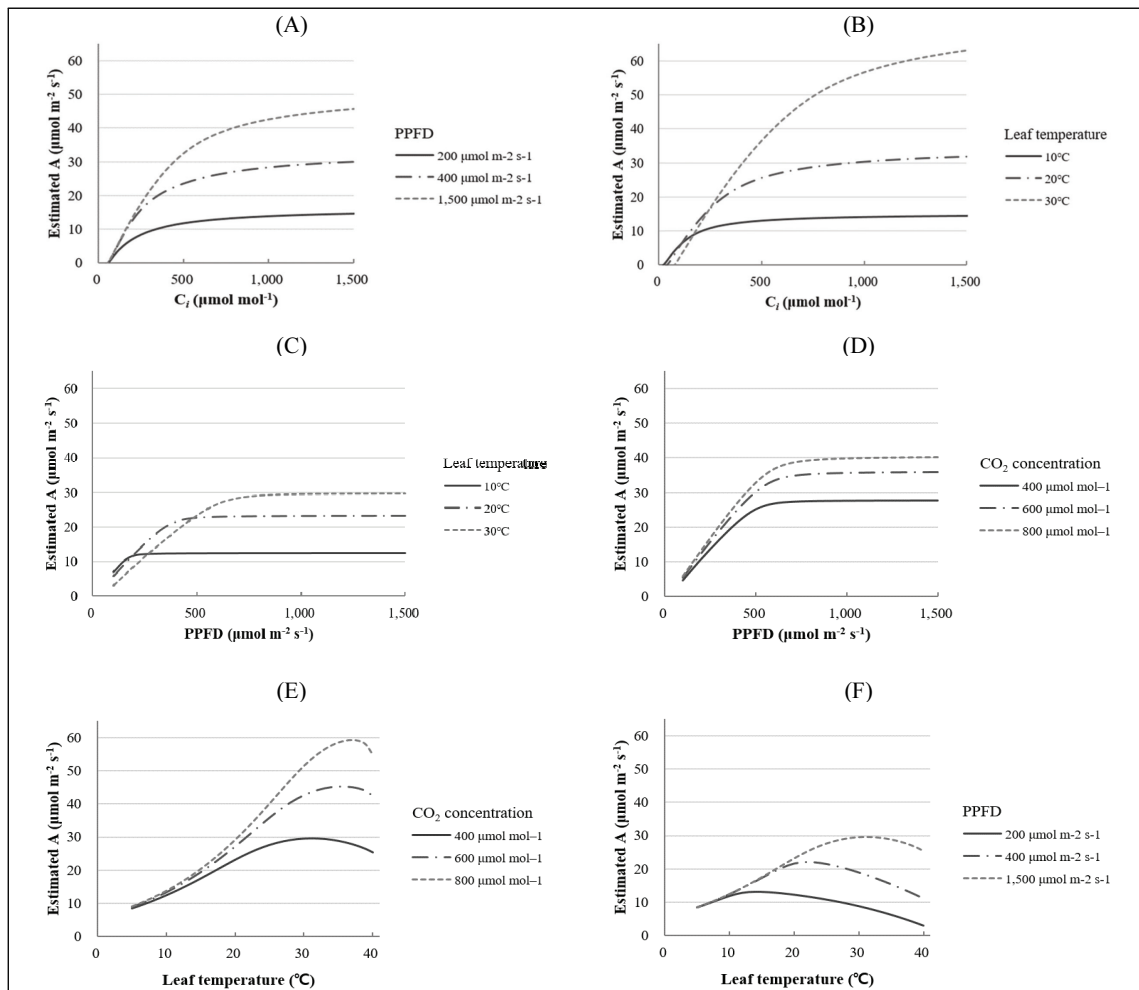


Fig. 2. Estimated net CO₂ assimilation rates (A) by leaf gas-exchange model for onion leaves (Photosynthetic photon flux density = 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, air temperature = 25°C, RH = 60%, wind speed = 0.5 m s^{-1}).

acclimation of carboxylation capacity (Ainsworth and Rogers, 2007). Also, sufficient concentration of CO₂ (up to 1,000 μmol mol⁻¹ CO₂) may enhance total leaf area, root dry weight, root volume, and specific leaf weight (Urban and Restrepo-Diaz, 2017). Meanwhile, the CO₂ compensation points generally increase with increasing temperature as shown in Figure 2B, and most C₃ plants such as lettuce, tomato, and wheat have CO₂ compensation points of 40~100 μmol mol⁻¹ (Nobel, 2009).

The increases in *A*, as well as light saturation point, with increasing temperature were observed in this study (Fig. 2C). The increases in *A* with CO₂ concentration (Fig. 2D) were considered as a result of the disappearance of the limiting factors in carboxylation. Meanwhile, the better photosynthetic performance at high temperature (35~40°C in sweet orange) was supported by higher photochemical efficiency in both light and temperature response curves (Ribeiro *et al.*, 2006).

The temperature response curves estimated by gas-exchange model at each CO₂ concentration were shown in Figure 2E. Since onion is known as a cool-weather crop, grown in USDA zones 3 to 9, high temperatures or other stressful conditions can cause bolting (Rhoades, 2013). The estimated rates of photosynthesis at ambient CO₂ concentration (400 μmol mol⁻¹) showed a decline with increasing temperature above 30°C. Similar result was reported in garlic, another cool-season crop that is commonly planted in late fall or early winter in temperate regions (Kamenetsky, 2007), indicating an adaption to cooler temperatures in ambient CO₂ concentration. The gas-exchange model explains that primary limitation in CO₂ assimilation under low temperatures (less than 13°C) in saturating light is related with triose phosphate utilization (*A_p*) in both ambient and high CO₂ concentrations (Kim *et al.*, 2013). Meanwhile, optimum temperature in photosynthesis showed a clear shift to high temperature with increasing CO₂ concentration. The competitive inhibition of CO₂ assimilation by photorespiration at high temperatures is often alleviated by high CO₂

concentration in many C₃ plants (Kim and Lieth, 2003; Sage and Kubien, 2007). In addition, there were optimal temperature shifts associated with increased irradiance (Fig. 2F). Similarly, large upward shifts in the temperature optimum of canopy gross photosynthesis were reported at high irradiances, following the response of *A_{sat}*, in non-rectangular hyperbola model for simulating the effect of temperature and CO₂ responses of leaf and canopy photosynthesis (Cannell and Thornley, 1998).

IV. Conclusion

V_{cmax}, *J_{max}*, *TPU*, and *R_d*, main parameters of leaf gas-exchange model, were estimated using FvCB model based on biochemical photosynthetic mechanisms and the measured value of net photosynthesis in onion grown in a temperature gradient plastic film house. After parameterization, model calibration was carried out to minimize the differences between estimated and measured values. The accuracy of the model completed through modification showed a confidence of 95.2%. Therefore, this model is expected to be successfully incorporated into comprehensive process-based model by enabling accurate prediction of leaf photosynthesis in the future.

적 요

식물의 생리적 과정과 환경 요인 간 상호작용에 바탕을 둔 프로세스 모형은 작물 생육 및 생산성 예측을 위한 좋은 도구이다. 탄소 획득과 바이오매스 증가는 프로세스 모형 개발의 주요 구성요소로서, 작물모형 내에서 광합성 과정의 이해 및 통합에 중요한 역할을 한다. 본 연구는 1980년 Farquhar 등에 의해 제안된 C₃ 식물 잎의 광합성 모델인 FvCB 모형의 양파에 대한 적용 가능성 평가 및 적합한 모수 추정을 목표로 수행되었다. 이를 위해 온도구배하우스에서 재배된 조생종 양파 품종인 ‘싱싱볼’과 ‘썬더볼’의 광합성 측정 결과를 바탕으로 *V_{cmax}*, *J_{max}*, *TPU* 및 *R_d* 값을 추정하였다. 본 연구에서 개발된 양파의 기체교환 모형은 다양한 환경 조건에서 양파의 광합성 반응 예측 및 설명에

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