

A Model for Predicting the Effect of Increasing Air Temperature on the Net Photosynthetic Rate of *Quercus mongolica* Stands

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ABSTRACT: A model was developed to predict the effects of rising air temperature on net photosynthetic rate of *Quercus mongolica* stands at Mt. Paekcheok-san, Kangwon-do in South Korea. The PFD (Photon flux density) and air temperature were determined from weather data from the research site and the Daegwallyeong meteorological station and gas exchange or release responses of each tree component were measured. Using these data, we simulated the effects of increases in mean annual air temperatures above current conditions on annual CO₂ budget of *Q. mongolica* stands. If mean annual air temperature is increased by 0.5, 1.0, 1.5, 2.0, 2.5 or 3.0 °C, annual net photosynthetic rate will be increased by 8.8, 12.8, 14.5, 12.6, 9.2 and 1.0 ton CO₂ ha⁻¹ yr⁻¹, respectively. Simulations indicate that changes in air temperature will have a major impact on gas exchange and release in *Q. mongolica* stands, resulting in a net increase in the rate of carbon fixation by standing crops.

Key words: Net photosynthetic rate, *Quercus mongolica*, Rising air temperature, Simulation model

INTRODUCTION

Oak species are dominant components of forest communities throughout the Korean peninsula. In Korea, *Quercus mongolica*, *Q. aliena*, *Q. variabilis*, *Q. serrata*, *Q. acutissima* and *Q. dentata* are the most common tall deciduous oaks in the cool temperate zone (Han and Kim 1989, Kim and Kim 1994, Song et al. 1995, Ihm et al. 2003). These species are dominant on xeric and shallow forest soils, but are also occasionally observed in other environments. *Q. mongolica* is an edaphic climax species in broad-leaved deciduous forests in the cool temperate zone, and is most often found on mesic north- and east-facing aspects and higher and middle slopes having moderately deep soils.

Climate models predict that global temperatures will increase in the future. Over the past 100 years, the global mean surface air temperature has increased by approximately 0.5 °C and recent evaluations by the IPCC (<http://www.ipcc.ch/pub/reports.htm>) based, in part, on an assessment by the US National Academy of Sciences, have indicated that projected rises in atmospheric CO₂ and associated greenhouse gases could lead to a 3~12 °C increase in global surface temperature during this century. Plants growing in temperate climates will more often be exposed to high temperature conditions (Haldimann and Feller 2004). Previous studies have focused on the responses of oak forests to specific environmental changes. In this

study, we use field data and simulation models to predict the response of the rate of net photosynthesis of *Q. mongolica* stands to rising air temperatures due to global warming. Simulation models are important tools for such work, allowing researchers to integrate ecological information across spatial and temporal scales (Caldwell et al. 1986, Reich et al. 1990, Suh 1996, Kim and Kim 1997, Infante et al. 1999, Ihm et al. 2001).

The objectives of this study are (1) to model and evaluate gas exchange and release responses of *Q. mongolica* stands to changes in temperature, (2) to use this model to simulate these responses under different mean annual air temperatures, and (3) to predict the effects of rising air temperature on net photosynthetic rates of *Q. mongolica* stands.

MATERIALS AND METHODS

The study area was Mt. Paekcheoksan, Pyeongchang-gun, Kangwon-do (N 37°33', E 127°30', 960 m above sea level) in Korea. We worked in *Q. mongolica* forests, which are composed of a herbaceous layer (annual and perennial species), a shrub layer, and a canopy layer consisting of approximately 50-year-old *Q. mongolica* (deciduous oak) trees, which are on average about 15 m in height, and 17 cm diameter at breast height (Ihm et al. 2003). Average tree density in this area is approximately 1,086 trees ha⁻¹. This area has a temperate climate with four distinct seasons and about two-thirds

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of the annual precipitation occurs between June and September. In *Q. mongolica* communities, *Stephanandra incisa*, *Viola rossii*, *Carex lanceolata*, *Melampyrum roseum*, *Polygonatum odoratum* var. *pluriflorum*, *Carex siderosticta*, *Aster scaber* and *Spodiopogon sibiricus* are dominant, and vascular plant species richness was 121 species (Lee and Kim 1994).

The vegetation structure, the light intensity in the canopy, and gas exchange by *Q. mongolica* leaves were surveyed at the study site on Mt. Paekcheoksan. The relative light intensity was determined using methods described by Kim (1985). The vertical and the horizontal light intensities in the canopy were then calculated from these measured values using the Lambert-Beer Law (Monsi and Saeki 1953, Ihm et al. 2001). Gas exchanges of leaves, twigs and roots were measured with saplings acclimated for 1 year in a greenhouse. Carbon dioxide release was measured using an infra-red gas analyzer (ADC, UK).

Model Description

Gas exchange or release responses for each tree component were determined and then combined with the biomass for the respective component to obtain a quantitative estimate of the total gas exchange or release. Climatic variables were hourly values of PFD (Photon flux density) and daily maximum and minimum temperatures in 1993 ~ 1997 (Kim et al. 1986, Kim and Kim 1997). A modified version of Suh's model (1992) for estimation of carbon dioxide budgets in an oriental arborvitae (*Thuja orientalis*) population was employed to calculate gas exchange or release rates for each plant organ every hour using measured PFD and air temperatures. The calculated hourly rates were then summed up to produce daily and annual outputs (Fig. 1). Symbols, definitions and units for the model are shown in Table 1.

Diurnal Pattern of Climatic Variables

The daily PFD cycle was approximated using the method of Anderson (1971) and was corrected for cloud cover according to O' Rourke and Terjung (1981). The daily temperature cycle was approximated by the sinusoidal equation using known daily maximum and minimum temperatures (Suh 1996).

Estimates of the Mass of Each Part of Trees

To estimate the mass of each *Q. mongolica* tree part per unit area (ton/ha), diameters at breast height and heights of all trees in 600 m² of the research site were measured and then the estimated mass of each plant part were determined according to the allometric equation of Kwak and Kim (1992).

$$\log W_l = 0.808 \log (D^2H) - 2.413 \quad (1)$$

$$\log W_b = 1.017 \log (D^2H) - 2.476 \quad (2)$$

$$\log W_s = 1.096 \log (D^2H) - 2.029 \quad (3)$$

where W_l is the leaf mass, W_b the branch mass and W_s the stem

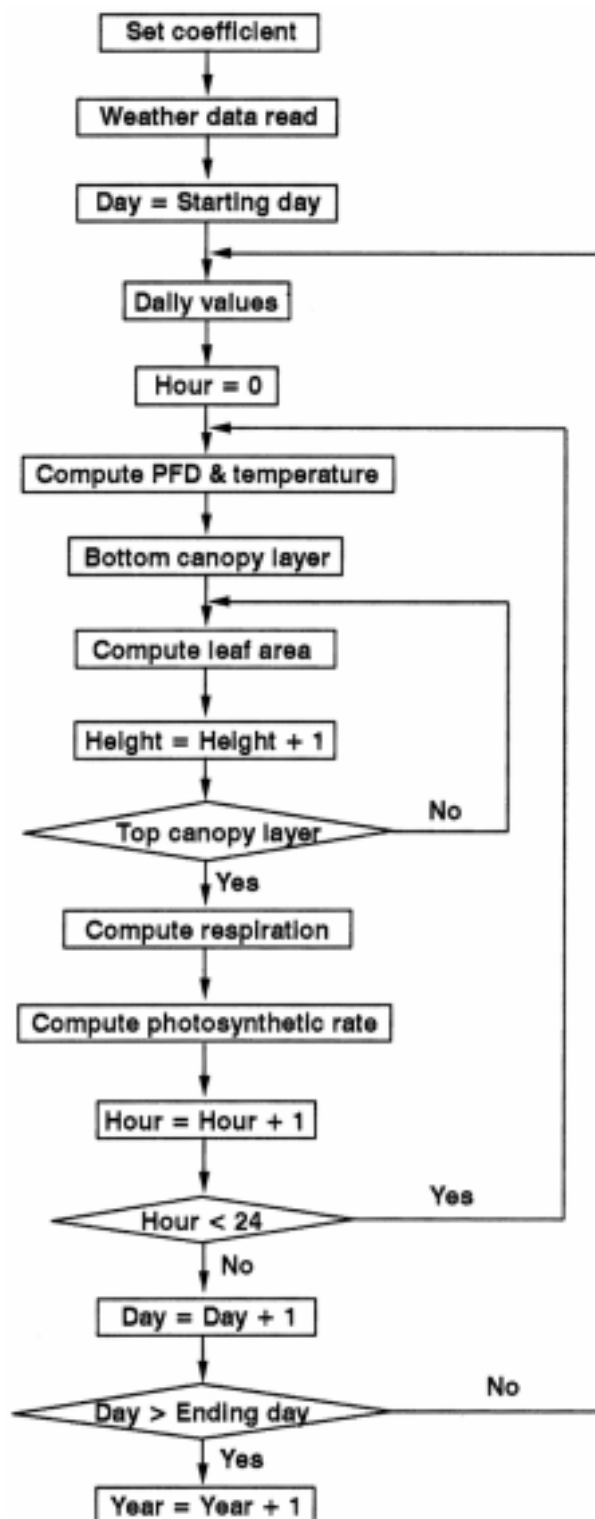


Fig. 1. Model flow-chart illustrating the main computational steps.

Table 1. Symbols, definitions and units of the model

Symbol	Description	Unit
D	Day in a given year	day
H	Hour in a given day	hour
H_t	Height of stem	m
K	Gross photosynthetic rate	mg CO ₂ dm ⁻² hr ⁻¹
K_{LA}	Maximum leaf area index $\times 10^4$	m ²
LA_D	Leaf area on a given day	m ²
LA_z	Leaf area at height z	m ²
$P(Q, T)$	Photosynthetic rate at a given Q and T	mg CO ₂ dm ⁻² hr ⁻¹
P_n	Net photosynthetic rate	mg CO ₂ dm ⁻² hr ⁻¹
P_x	Maximum net photosynthetic rate	mg CO ₂ dm ⁻² hr ⁻¹
Q	Photon flux density (PFD)	mmol quanta m ⁻² s ⁻¹
R	Respiration rate	mg CO ₂ g ⁻¹ DM hr ⁻¹
R_b	Respiration rate of branches	mg CO ₂ g ⁻¹ DM hr ⁻¹
R_l	Respiration rate of leaves	mg CO ₂ dm ⁻² hr ⁻¹
R_r	Respiration rate of roots	mg CO ₂ g ⁻¹ DM hr ⁻¹
R_s	Respiration rate of stems	mg CO ₂ g ⁻¹ DM hr ⁻¹
$R(d, T)$	Respiration of stems at a given d and T	mg CO ₂ g ⁻¹ DM hr ⁻¹
T	Air temperature	°C
W	Dry matter	g
W_b	Dry matter of branches	g
W_l	Dry matter of leaves	g
W_s	Dry matter of stems	g
c	Integration coefficient	-
d	Diameter of stem	cm
r_{LA}	Growth coefficient of leaf area	-

mass. D is the diameter at breast height and H is the tree height. The underground biomass was assumed to be 25 percent of above-ground biomass (Madgwick 1982). Standing crops for each plant part in *Q. mongolica* stands at the research site are given in Table 2.

Leaf Dynamics

We modeled seasonal leaf dynamics using LA_D and time constant D using the logistic equation based on the data of Min (1994a, b). The leaf area distribution (LA_z) with height (z) was fitted to the equation using a quadratic function.

Respiration

The relationship between the rate of respiration of leaves (R_l , mg

Table 2. Standing crops of each part of *Q. mongolica* trees

Part	Standing crop (ton/ha)
Leaves	4.1
Branches	22.3
Stems	129.3
Roots	38.9
Total	194.6

dm⁻² hr⁻¹), roots (R_r , mg g⁻¹DM hr⁻¹) and branches (R_b , mg g⁻¹DM hr⁻¹) and ambient temperatures was approximated using the following exponential equations:

$$R_l = \exp(-1.128 + 0.017 T) \quad (r=0.991, n=91) \quad (4)$$

$$R_r = \exp(-2.118 + 0.044 T) \quad (r=0.959, n=102) \quad (5)$$

$$R_b = \exp(-2.359 + 0.062 T) \quad (r=0.999, n=50) \quad (6)$$

The rate of respiration of stems decreased with stem diameter and increased with temperature. The relationship between the rate of respiration of stems and stem diameter and temperature was approximated using the following exponential equation:

$$R(d, T) = \exp(-1.888 - 0.224 d + 0.056 T) \quad (7) \\ (r=0.941, n=268)$$

As the stem diameter in a tree decreased with height the respiration rate per unit area increased. Thus, the rate of respiration of the stem of a tree can be described as:

$$R_s = R(d, T) \times W_s \quad (8)$$

The rate of respiration for each stem in the study stands was calculated and these results were added to derive an estimated rate of respiration for all *Q. mongolica* trees at the research site.

Net Assimilation Rate

The net assimilation rate was calculated using the equation of Potvin et al. (1990):

$$P(Q, T) = K \{1 - \exp(-fQ)\} + R_l \quad (9)$$

where $P(Q, T)$ is the photosynthetic rate at a given Q and T (mg CO₂ dm⁻² hr⁻¹), K is gross photosynthetic rate (mg CO₂ dm⁻² hr⁻¹) and R_l is respiration rate of leaves (mg CO₂ dm⁻² hr⁻¹). The constant f was estimated as -2.355 using regression of the net assimilation rate and PFD in optimum temperature.

Assuming that PFD is very large we may modify Eq. 9 to:

$$P(\infty, T) = K + R_1 = P_x \quad (10)$$

Under saturating PFD the relationship between leaf photosynthesis and temperature (P_x , mg CO₂ dm⁻² hr⁻¹) was approximated using the quadratic function (Anderson 1982):

$$P_x = -24.930 + 3.071 T - 0.052 T^2 \quad (11)$$

(r=0.957, n=98)

RESULTS

Gas Exchange

The optimum temperature for photosynthesis of *Q. mongolica* leaves was 27~30°C, which is similar to reported optimum temperatures of 24, 23 and 26°C of *Q. rubra*, *Q. pubescens* and *Q. glauca* (Jurik et al. 1988, Larcher 1969) and 25°C for *Q. aliena*, *Q. variabilis* and *Q. serrata* (Han and Kim 1989). The highest temperature for photosynthesis of *Q. mongolica* leaves was 42°C, which is consistent with reported maximum temperatures of 45 and 42°C for *Q. pubescens* and *Q. ilex*, respectively (Larcher 1969). The maximum net photosynthetic rate of *Q. mongolica* leaves at 30°C was 20.2 mg CO₂ dm⁻² hr⁻¹, which is similar to reported rates of 26.6 and 18.1 mg CO₂ dm⁻² hr⁻¹ for *Q. lobata* and *Q. rubra* (Hollinger 1992, Jurik et al. 1988) and 19.7, 15.2 and 11.0 mg CO₂ dm⁻² hr⁻¹, respectively, for *Q. variabilis*, *Q. serrata* and *Q. aliena* (Han and Kim 1989). The respiration rate of *Q. mongolica* leaves at 25°C was 0.49 mg CO₂ dm⁻² hr⁻¹ which is lower than reported rates of 0.80, 1.97 and 1.21 mg CO₂ dm⁻² hr⁻¹ for *Q. pubescens*, *Q. lobata* and *Q. agrifolia*, respectively (Larcher 1969, Hollinger 1992). The respiration rate of *Q. mongolica* stems and roots at 25°C were 0.09~0.45 and 0.37 mg CO₂ g⁻¹DM hr⁻¹, respectively.

Carbon Dioxide Budget

Using the estimated daily PFD and air temperature cycles, we calculated gas exchange or release rates for leaves, roots, stems and branches. Fig. 2 compares the P_n measured at the research site and the P_n predicted from the model. The correlation between the measured P_n and the predicted P_n was statistically significant ($P < 0.001$):

$$\text{Predicted } P_n = 0.922 \text{ Measured } P_n + 0.370 \quad (r=0.973, n=64)$$

The highest daily total respiration rates for leaves, roots, stems and branches in *Q. mongolica* stands were -98.7, -293.2, -85.8 and -195.8 (33.7: 100: 29.3: 66.8) kg CO₂ ha⁻¹ day⁻¹. The lowest

daily respiration rates of roots, stems and branches were -62.8, -12.5 and -22.6 (100 : 19.9 : 36.0) kg CO₂ ha⁻¹ day⁻¹. The highest daily net photosynthetic rate was 1,210.5 kg CO₂ ha⁻¹ day⁻¹. The annual gross productivity, total respiration rate and net productivity of *Q. mongolica* stands were 222.0, 121.6 and 100.4 ton CO₂ ha⁻¹ yr⁻¹ (Table 3).

We have developed a numerical model for estimation of the effects of rising air temperature on net photosynthetic rate of *Q. mongolica* stands (Suh 1992, Kim and Kim 1997, Kim et al. 1999). The annual CO₂ budget of *Q. mongolica* stands was simulated under conditions of mean annual air temperatures higher than the present condition (Fig. 3). If mean annual air temperature is increased by 0.5, 1.0, 1.5, 2.0, 2.5 and 3.0°C, we calculated that the annual net photosynthetic rate will increase by 8.8, 12.8, 14.5, 12.6, 9.2 and 1.0 ton CO₂ ha⁻¹ yr⁻¹ (9, 13, 15, 13, 9 and 1%), respectively. Therefore, our simulations predict that increasing the air tempera-

Table 3. Annual carbon dioxide budget (ton CO₂ ha⁻¹ yr⁻¹) of *Q. mongolica* stands at the research site

	ton CO ₂ ha ⁻¹ yr ⁻¹
Stand respiration	
Leaves	-13.1
Roots	-59.9
Stems	-15.6
Branches	-33.0
Subtotal	-121.6
Net productivity	100.4
Gross productivity	222.0

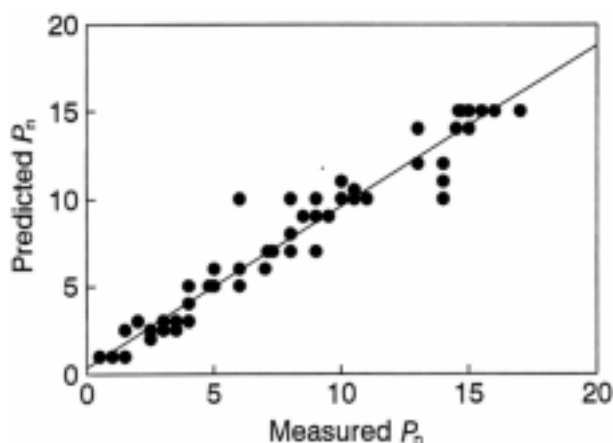


Fig. 2. The relationship between the P_n measured at the research site and the P_n predicted by the model.

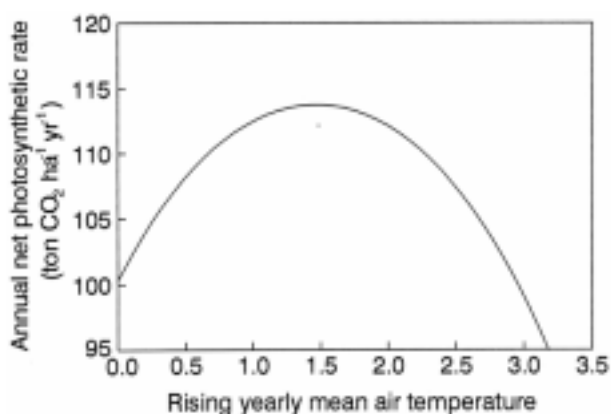


Fig. 3. Changes in the annual net photosynthetic rate of *Q. mongolica* stands in response to rising air temperatures predicted by the simulation model.

ture above the present condition will have a substantial impact on gas exchange and release in *Q. mongolica* stands and will result in net increase in carbon fixation by the forest canopy.

DISCUSSION

Net photosynthetic rates of *Q. mongolica* forests at the research site were affected by changes in mean annual air temperatures during simulated climate change (Fig. 3). Our results suggest that elevated air temperatures will result in an increase in the net carbon gain by *Q. mongolica* stands. These effects are complex, suggesting that ecosystem models should explicitly simulate the biological processes by which air temperature, CO₂ concentrations, PFD and water stress affect net and gross productivity at a time scale appropriate to the large diurnal variation in these effects (Fig. 1). Changes in net and gross productivity will also drive changes in litter fall and heterotrophic respiration (Grant et al. 2003).

Elevated growth temperatures have been shown to increase the relative response of photosynthesis to elevated CO₂ in other studies (Callaway et al. 1994, Kellomäki and Wang 1996, Koike et al. 1996), as is predicted based on the effects of increasing temperature and CO₂ on the carboxylation efficiency of Rubisco (Long 1991). Elevated growth temperature has also been shown to enhance photosynthetic responses to elevated CO₂ by increasing needle N (Kellomäki and Wang 1997, Lewis et al. 2004). Growth in elevated temperature significantly increased chlorophyll concentrations (Ormrod et al. 1999). Increased needle N with increased growth temperatures may result from increased soil nitrogen availability due to increased soil nitrogen mineralization rates (Rygielwicz et al. 2000), as has been observed in other studies (van Cleve et al. 1990, van Breemen et al. 1998). Rising soil temperature may amplify the effect of

elevated CO₂ concentrations on net and gross primary productivity (Oechel et al. 1994). The modelled change in species composition was consistent with findings from several field experiments by Shaver & Jonasson (1999) that higher temperatures cause increased production of vascular plants. Other studies have also suggested some of the potential impacts of an increase in the number of hot days and/or changes in average annual temperatures on plant organs (Atkin et al. 2000).

In this study, we have not considered the complex relationship between photosynthesis and environmental factors such as soil nutrients, rainfall, hydrology, and the impact of these factors on interactions between temperature and ecophysiological processes following global warming (Fig. 1). However, in simulations of gas exchange in *Q. coccifera* shrubs, Tenhunen et al. (1990) were able to effectively describe annual changes in net photosynthesis by varying several factors. Our research may also be utilized to describe many of the non-linear effects of light and temperature on leaf photosynthesis (Harley et al. 1986, McMurtrie et al. 1992, Tenhunen et al. 1994, Sala and Tenhunen 1996).

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