

Comparison of Two Numerical Models on Photosynthetic Response of *Quercus mongolica* Leaves to Air Pollutants

Joon-Ho Kim¹, Byung Sun Ihm^{2*}, and Jong Wook Kim²

¹Department of Biology, Seoul National University, Seoul 151-742, Korea

²Department of Biology, Mokpo National University, Muan-Cun 534-729, Korea

A multiple-regression model is presented for estimating the effect of major air pollutants on net photosynthetic rate (Pn) of *Quercus mongolica* leaves, of which visible injury is not shown. Photosynthetic capacity was found to be primarily a function of PPF, air temperature (T) and ambient ozone (O₃) concentration. The negative direction of photosynthetic capacity response to O₃ concentration indicates a potential growth reduction of *Q. mongolica* due to ambient O₃ concentration in the urban areas of Korea. The model was compared with a non-linear regression model including the same variables. We assessed the contribution of variables to two models of ambient O₃ affecting Pn of *Q. mongolica* leaves. The mean Pn difference between the models with and without ambient O₃ in the multiple-regression was smaller than that in the non-linear regression. The relative contributions of ambient O₃ to multiple-regression and non-linear regression were 12.6% and 5.6%, respectively. The results indicate that multiple-regression models can be applicable for qualitative or quantitative assessment of the effect of air pollutants on Pn response of plant leaves, of which visible injury may not be shown in situ. Also, the assessment of ecophysiological effects using numerical models will have a degree of uncertainty associated with the measuring time/period of the field data used in the modelling, as well as the numerical structure of the models.

Key words: *Quercus mongolica*, Photosynthesis, Air pollutant, Multiple regression, Non-linear regression

Ambient O₃ with other photochemical oxidants has been known to directly inflict foliar injury and premature loss (Heck et al., 1982, 1983; Reich and Amundson, 1984, 1985; Reich and Rossoie, 1985; Hinrichsen, 1987; Kim and Kim, 1997). Also, O₃ exposure in combination with acid mist or fog may increase nutrient leaching from leaves or needles, and the resulting Mg and Ca deficiencies reduce photosynthesis and biomass production both in the canopy and in root systems (Prinz, 1987; Cook and Johnson, 1989; Rhyu and Kim, 1994a,b). Although ambient O₃ cannot explain all the characteristics and the causes of recent forest decline, it has been regarded as the primary cause in central Europe, North America and Asia (Heck et al., 1984a,b; Miller, 1989; Kim and Kim, 1997). In fact, when visible injury of plants is not shown, it is difficult to detect and quantify the effects of air pollutants on plant response. Thus, we have been trying to verify and quantify the effects of O₃ with acid mist or fog with numerical models using ecophysiological data as a measure of tree response. These attempts may have the advantage that the effects of air pollutants on plant can be verified in situ.

Krupa and Kickert (1987) reviewed many numerical models between air pollutant exposure and vegetation response. Also, various models have been developed for trees and crop species to simulate the change of primary production by the air pollutants (Reich et al., 1990; Moldau et al., 1991; Mohren et al., 1992; Meldahl et al., 1992; Krupa et al., 1995; Kim and Kim, 1997). Here, we try to directly compare two kinds of numerical models used frequently in the analyses of plant ecophysiological responses affected by air pollutants. We developed a multiple-regression model using climatic and anthropogenic factors affecting Pn and compared it with non-linear regression model used by Kim and Kim (1997). First, for developing the multiple-regression model, various statistical methods were carried out, such as ridge regression, and forward stepwise selection by the least-squares method (Meyers, 1990; SAS, 1993). To estimate and compare the mean Pn difference in each model, the mean value divided by the sum of the Pn difference between the models with and without air pollutants by the number of observations, the bootstrap and jackknife procedures were used for the two models, respectively. These procedures have been used to estimate the precision of various similarity measures, including measures of population growth rate (Brault and Caswell, 1993), diet similarity

*Corresponding author; fax +82-636-454-0267
e-mail ihmbs@chungkye.mokpo.ac.kr

(Smith, 1985), community similarity (Smith et al., 1986) and niche overlap (Manly, 1990). Recently, they have been preferred as very useful powerful analysis techniques.

The purposes of this paper are: 1) to verify and quantify the effects of major air pollutants with numerical models using ecophysiological data such as Pn (net photosynthetic rate), and 2) to compare the contribution of air pollutants affecting Pn of *Quercus mongolica* leaves to the two models, and to compare the numerical characteristics of the two models.

METHODS

Leaf Gas Exchange and Air Pollutants

Q. mongolica trees about 50 years in age, 15 m in height, 19 cm in mean diameter at the breast height, and at a density of about 950 trees per ha were used as material plants. These were growing at Mt. Namsan Park (37°33'N, 127°00'E, 250 m above sea level), a public natural park of Seoul, Korea (Kim and Kim, 1997; Hong and Nakagoshi, 1998).

Carbon dioxide uptake of leaves was measured with a portable infra-red gas analyser (LCA2, ADC, UK) connected to a leaf chamber with an integral humidity sensor, thermistor and quantum sensor (PLC, ADC). Air was supplied to the leaf chamber from a stabilized collection point placed outside the canopy and the flow rate measured with an air flow pump and mass flow meters/controllers (ASU, ADC). Uptake rates of CO₂ were calculated using the equation of Long and Hallgren (1985). Measurements were made at monthly intervals from June to September 1993 in situ. In each measurement, ten leaves, which were perfectly expanded at the outer layer of canopy from five individuals, were selected at random.

The hourly average concentrations of TSP (total suspended particulate), SO₂, NO₂ and O₃ recorded at the National Air Pollution Monitoring Station at nearby Hannam-dong in Seoul were used as the data of air pollutants.

Statistical Analysis

The contribution of climate factors such as hourly average PPF and air temperature and air pollution factors such as hourly average TSP, SO₂, NO₂ and O₃ concentrations to Pn of *Q. mongolica* leaves were analyzed by multiple-regression analysis (Meyers, 1990).

In multiple-regression analysis, the strong collinearity among the independent variables prevents ordinary least squares from providing meaningful estimates of the model parameters and in detecting multicollinearity the diagnosis involved several aiding procedures (Meyers, 1990): the eigenvalue (or ratio) to assess the seriousness of a particular dependency, the variance proportions to signify what variables are involved in the dependency and to what extent, and the variance inflation factors (VIFs) to aid in determining the damage to the individual coefficients. Multicollinearity can be measured in terms of the ratio of the largest to the smallest eigenvalue, e.g. when the condition number of the correlation matrix exceeds 1,000 one should be concerned about the effect of multicollinearity. It is generally accepted that if any VIF exceeds 10, a more suitable method should be considered. A small eigenvalue (serious linear dependency), accompanied by regressors with high variance proportions, represents a dependency involving the regressors, and the dependency is damaging to the precision of estimation of the coefficients.

Ridge regression may provide better parameter estimates when multicollinearity is detected in multiple-regression models. The multiple-regression model is modified by adding an extra parameter, k , which limits the length of the regression coefficient vector (Hoerl and Kennard, 1970). The analysis is based on the change in coefficient values as a function of k (the ridge trace). The variables are selected from the results of ridge regression.

We also used forward stepwise selection by the least-squares method (SAS, 1993). The forward selection technique begins with no variables in the model. This calculates F statistics reflecting a variables contribution to the model if it is included. These F statistics are compared to the 5% significance level for entry into the model. If no F statistic has a significance level greater than the 5% level, forward stepwise selection stops. Otherwise, forward stepwise selection adds the variable that has the largest F statistic to the model. The model selection criteria are the coefficient of determination (R^2) or Mallows' C_p statistic (Meyers, 1990). R^2 is a measure of the model's capability to fit the present data. However, the insertion of any new regressor into a model cannot bring about a decrease in R^2 . When C_p is graphed with p , the model where C_p first approaches p is recommended. When the right model is chosen, the parameter estimates are unbiased, which is reflected in C_p nearing p .

For the selected model, analysis of the residual is carried out to detect and assess the degree of discrep-

Table 1. Correlation coefficients among the Pn and the six predictor variables used in regression analysis (N=68). ISP= total suspended particulate; PPFD=photosynthetic photon flux density; T=air temperature; Pn=Net assimilation rate.

	ISP	ln(ISP)	O ₃	ln(O ₃)	SO ₂	ln(SO ₂)	NO ₂	ln(NO ₂)	PPFD	ln(PPFD)	T	ln(T)
O ₃	-0.089	0.122										
ln(O ₃)	-0.086	0.122										
SO ₂	0.740***	0.568***	-0.231	-0.276*								
ln(SO ₂)	0.651***	0.527***	-0.212	-0.254*								
NO ₂	0.662***	0.653***	-0.003	-0.072	0.418***	0.428***						
ln(NO ₂)	0.602***	0.647***	0.093	-0.016	0.407***	0.444***						
PPFD	-0.015	0.103	-0.096	0.016	0.060	0.066	-0.214	-0.137				
ln(PPFD)	-0.010	0.062	-0.216	-0.123	0.095	0.118	-0.129	-0.102				
T	-0.076	0.152	0.194	0.255	-0.346**	-0.336**	-0.022	0.004	0.568***	0.550***		
ln(T)	-0.058	0.167	0.198	0.257	-0.352**	-0.339**	0.003	0.019	0.543***	0.526***		
Pn	0.059	0.119	-0.309	-0.237	0.159	-0.153	-0.035	0.051	0.693***	0.841***	0.481***	0.461***

* P<0.05; ** P<0.01; *** P<0.001.

any between the model assumed and the data observed.

The independence of residuals was checked by Durbin-Watson test (SAS, 1993). The aim of this test is to check whether or not the errors have first-order autocorrelation. If the Durbin-Watson statistic (*d*) is close to 2, it is suggested that the errors do not have first-order autocorrelation. The homogeneous variance of residuals was checked by residual against predicted value plot (SAS, 1993). If the plot indicates a random pattern around zero with no detectable trend, the homogeneous variance assumption of the errors are accepted. The normality of the errors was checked by Shapiro-Wilk statistic (*W*) (Shapiro and Wilk, 1965). The statistic (*W*) can determine whether to reject the null hypothesis of normality. It is only necessary to examine the probability associated with the test statistic. This probability is described *p*<*W* for the test. If this value is less than the chosen level, then the null hypothesis is rejected and we can conclude that the data do not come from a normal distribution. The *W* statistic is the ratio of the best estimate of the variance to the usual corrected sum of squares estimator of the variance.

For a test of the null hypothesis of the observed value and the value predicted by the selected multiple-regression ($H_0: \mu_d = 0$), the t-test is carried out (SAS, 1993).

Comparison of Two Numerical Models

Kim and Kim (1997) developed a non-linear regression model predicting the ambient O₃ effect on the Pn of *Q. mongolica* leaves. Net photosynthetic rate $P(Q, T)$ at a given PPFD (*Q*) and air temperature (*T*) can be calculated as follows:

$$P(Q, T) = P_g \{1 - \text{EXP}(-iQ)\} - R_l \tag{1}$$

where P_g , *i* and R_l are gross photosynthetic rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$), negative constant and leaf respiration rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$), respectively.

In the model with ambient O₃,

$$P(Q, T, C) = P_g P_{O_3, C} \{1 - \text{EXP}(-2.3548Q)\} - R_l \tag{2}$$

where *C* is ambient O₃ concentration (ppb) and $P_{O_3, C} = C^{0.001}$.

To estimate the contribution of ambient O₃ in the model, their mean Pn difference (μ_{d1} , $\mu\text{mol m}^{-2}\text{s}^{-1}$) was estimated using the measured data and calculating their Pn difference (*d1*) between the values calculated in the model with ambient O₃ by Eq. (2) and the model without ambient O₃ by Eq. (1).

$$d1 = P(Q, T) - P(Q, T, C) \tag{3}$$

$$\mu_{d1} = \left\{ \sum_1^n d1 \right\} / n = \left\{ \sum_1^n (P(Q, T) - P(Q, T, C)) \right\} / n \tag{4}$$

where *n* is the number of observations.

For the multiple-regression model selected, the mean Pn difference (μ_{d2} , $\mu\text{mol m}^{-2}\text{s}^{-1}$) was estimated by the same equation as Eq. (4), calculating their Pn difference (*d2*) in the selected model with ambient O₃ and the model removing the variable O₃ from the selected model. The Pn difference (*d2*) represents a proportion of the contribution to the multiple-regression model of ambient O₃. From the above two numerical models, the mean Pn differences between the models with and without ambient O₃ were estimated by the above equations and then their standard errors and confidence intervals were estimated by the bootstrap and the jackknife methods (Mueller 1979; Efron, 1987; Potvin and Rolé, 1993).

RESULTS

In measuring data during the study period, the highest concentrations of TSP, O_3 , SO_2 , and NO_2 were $41 \mu\text{g}/\text{m}^3$, 67 ppb, 19 ppb and 62 ppb, respectively. The ranges of PPFD and T were $9\sim 1487 \mu\text{mol m}^{-2}\text{s}^{-1}$ and $18.0\sim 33.5^\circ\text{C}$, respectively.

Table 1 shows linear correlation coefficients among Pn and the six predictor variables used in regression analysis. Higher correlations were found among concentrations of TSP, SO_2 and NO_2 ($P < 0.001$), regardless of values of logarithm or observation. Correlation between concentrations of O_3 and NO_2 was not significant contrary to expectation, which may be due to time lag between their chemical responses in the atmosphere. Temperature (T) highly correlated with PPFD and SO_2 . The Pn was highly correlated with PPFD and T ($P < 0.001$), but was negatively correlated with O_3 concentrations ($P < 0.05$).

Table 2 shows multiple regression coefficients between the Pn and the six predictor variables. After logarithmic transformation to ensure a linear relationship, PPFD was integrated into the analysis. Logarithmic transformation of the other variables did not significantly change the results, so these variables

Table 2. Multiple regression coefficients between Pn and the six predictor variables used in regression analysis (N=68). SE, *P*, VIF and *R* represent standard error, significance probability, variance inflation factor and multiple correlation coefficient, respectively. Abbreviations of the other variables are the same as in Table 1.

Variable	Coefficient	SE	<i>P</i>	VIF
Intercept	-10.618	2.372	0.001	0.000
TSP	-0.003	0.005	0.518	3.771
O_3	-0.034	0.015	0.027	1.236
SO_2	0.116	0.093	0.218	3.711
NO_2	0.011	0.020	0.592	1.876
ln(PPFD)	2.039	0.289	0.001	2.307
T	0.191	0.114	0.100	2.659
<i>R</i>	0.861	-	0.001	-

were not transformed in the analysis. Coefficients of ln(PPFD), T, SO_2 and NO_2 , had positive values, but O_3 and TSP had negative values. The multiple correlation coefficient was high (0.861) ($P < 0.001$). However, coefficients between Pn and TSP, SO_2 and NO_2 were not significant ($P < 0.05$) and so were removed from the regression model (Table 2).

The VIFs of all variables did not exceed 10, but the smallest eigenvalue, 0.00344 with condition number = 1728.015, reflects a dependency that is very damaging to the precision of coefficient estimates of regressors T and intercept and, to a smaller extent, to the coefficients of SO_2 and ln(PPFD) (Table 3). Clearly, this dependency heavily involves these four regressors (Table 2). The impact of the second smallest eigenvalue (0.01933) is marginal since the condition number is 307.698. This dependency can be interpreted as one that affects ln(PPFD). Consequently, such dependency is very damaging to the precision of coefficient estimates of T, intercept, ln(PPFD) and SO_2 .

Because of the multicollinearity in the multiple-regression model as seen in Table 3, ridge regression analysis was carried out using the measured data. The change of estimates of regression coefficient as func-

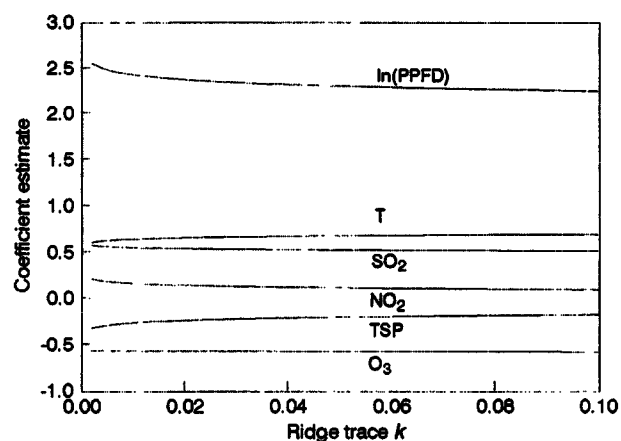


Figure 1. The ridge trace from ridge regression.

Table 3. Collinearity diagnostics. Abbreviations of the variables are the same as in Table 1.

Number	Eigenvalue	Condition number	Variance proportion						
			Intercept	TSP	O_3	SO_2	NO_2	ln(PPFD)	T
1	5.94781	1.000	0.0002	0.0022	0.0053	0.0015	0.0039	0.0005	0.0002
2	0.54362	10.941	0.0006	0.0480	0.1931	0.0136	0.0369	0.0012	0.0006
3	0.27346	21.750	0.0024	0.0199	0.4221	0.0073	0.1032	0.0143	0.0014
4	0.15217	39.087	0.0007	0.0617	0.1554	0.1140	0.5568	0.0012	0.0012
5	0.06017	98.850	0.0000	0.7128	0.0243	0.4335	0.2306	0.0049	0.0045
6	0.01933	307.698	0.2024	0.0027	0.1424	0.0001	0.0654	0.5329	0.0119
7	0.00344	1728.015	0.7936	0.1527	0.0574	0.4300	0.0032	0.4449	0.9802

Table 4. Multiple regression between Pn and the three predictor variables used in regression analysis (N= 68). Coefficients are estimated by the least-squares method. VII = variance inflation factor; R= multiple correlation coefficient; Abbreviations of the other variables are the same as in Table 1.

Variable	Coefficient	SE	P	VII
Intercept	-8.408	1.851	0.001	0.000
O ₃	-0.035	0.015	0.024	1.229
ln(PPFD)	2.189	0.247	0.001	1.696
T	0.109	0.091	0.234	1.680
R	0.853	--	0.001	--

tions of the ridge trace k from 0 to 0.1 is shown in Figure 1. Since the variables were standardized, coefficient amplitude could be compared directly. Most coefficient estimates stabilized quickly at about $k=0.02$. No matter what the k value was, the standardized coefficients of NO₂ and TSP kept near 0, while the coefficients of O₃, SO₂, T and ln(PPFD) were higher. In selecting model variables from this curve (Fig. 1), Hocking (1976) proposed that variables with a coefficient near zero or varying rapidly with k should be eliminated. This led us to eliminate NO₂ and TSP and select O₃, SO₂, T and ln(PPFD).

Forward stepwise selection added ln(PPFD), O₃, and T to the model one by one, and then finally SO₂ and stopped (Table 4). We kept the same variables in forward selection as those kept after ridge regression.

However, the coefficient between Pn and SO₂ was not significant ($P<0.05$) (Table 2) and SO₂ variable showed a positive effect to Pn, contrary to expectation. Thus, SO₂ variable was eliminated and finally the model including ln(PPFD), O₃, and T as regressors was selected. The multiple correlation coefficient was 0.853 and significant ($P<0.001$). This model could be compared with the numerical model of Kim and Kim (1997) including the same variables.

$$\text{Pn} = 2.189 \ln(\text{PPFD}) + 0.109 \text{T} \\ - 0.035 \text{O}_3 - 8.408 \quad (r = 0.853, n = 68).$$

For the selected multiple-regression model (Table 4), analysis of residual was carried out to detect and assess the degree of discrepancy between the model assumed and the data observed (Table 4). The Durbin-Watson test showed that the Durbin-Watson statistic ($d = 1.629$) was close to 2 and thus the residuals did not have first-order autocorrelation. A plot of residual against predicted value indicated a random pattern around zero with no detectable trend and thus the homogeneous variance assumption of the residuals was accepted. The Shapiro-Wilk statistic (W)

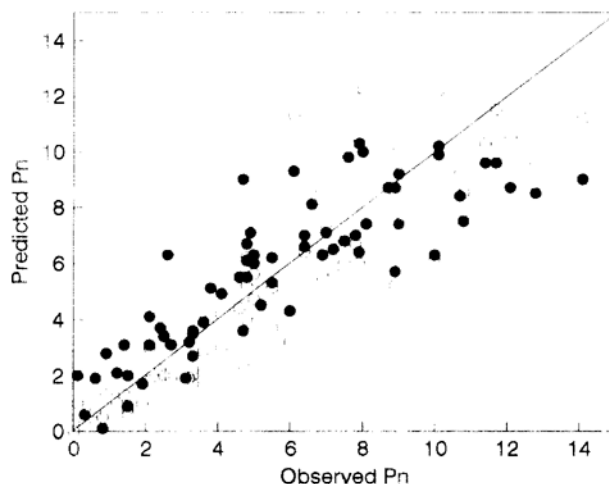


Figure 2. The relationship between the Pn observed and the Pn predicted by the multiple-regression model (○) and non-linear regression model (●). The diagonal line represents that predicted values are equal to observed ones.

showed that the data could not reject the null hypothesis of normality and thus followed the normal distribution.

Figure 2 compares both the Pn observed with the Pn calculated from the two predictive models, e.g. multiple-regression model (Table 4) and non-linear regression model (Kim and Kim, 1997). By the t-test on the null hypotheses that the observed values and the predicted values in each of two models were the same, the null hypotheses were not rejected ($P<0.990$ in the multiple-regression model and $P<0.537$ in the non-linear regression model).

The mean Pn difference (μ_{diff}) of the multiple-regression model selected above (Table 4) was compared with those (μ_{diff}) of the non-linear regression model including the same variables by Kim and Kim (1997), in order to verify the effect of ambient O₃ on Pn of *O. mongolica* leaves in the model. Their percent Pn reduction and mean Pn differences were estimated by the equations referred to in the Methods section (Table 5).

The mean Pn difference in the non-linear regression model ($\mu_{\text{diff}} = 0.319 \mu\text{mol m}^{-2} \text{s}^{-1}$) for the original data was smaller than that of the multiple-regression model ($\mu_{\text{diff}} = 0.806 \mu\text{mol m}^{-2} \text{s}^{-1}$). The contribution of ambient O₃ to the multiple-regression model and non-linear regression model was 12.6% and 5.6%, respectively. Meanwhile, for the estimates from small sample size of the observed data ($n=68$), the bootstrap procedure was used to quantify the precision and to calculate confidence intervals for the differences between the two mean Pn values. Using 1000

Table 5. The sample mean Pn differences (μ), the mean Pn differences (μ) by the bootstrap and the jackknife procedures, their standard errors, and the confidence intervals by the accelerated bootstrap method in non-linear regression and multiple-regression models. SE represents standard error. The number of bootstrap replicates is 1,000.

Model type	Sample mean μ	The bootstrap		The jackknife		Confidence interval	
		Mean μ	SE	Mean μ	SE	Lower limit	Upper limit
Non-linear regression	0.319	0.319	0.066	0.319	0.009	0.212	0.477
Multiple regression	0.806	0.809	0.074	0.806	0.009	0.665	0.954

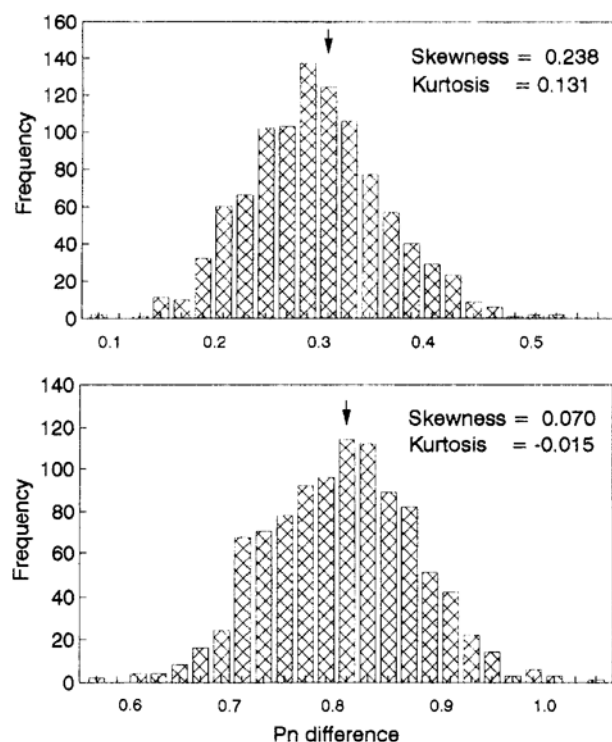


Figure 3. Frequency distribution of 1,000 bootstrap values for Pn differences between the models with and without O_3 in the non-linear regression model (above) and multiple-regression model (below). Arrow represents mean of 1,000 bootstrap differences in each model.

bootstrap samples, the mean differences in the non-linear regression model and multiple-regression model were 0.319 and 0.809 $\mu\text{mol m}^{-2}\text{s}^{-1}$, and the biases in each model were estimated to be 0.000 and 0.003, respectively, small in both cases. Using the jackknife samples, the mean differences were 0.319 and 0.806 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively, being equal to the sample mean differences.

The standard errors of the mean Pn difference were estimated by both procedures of bootstrap and jackknife procedures (Table 5). Using 1000 bootstrap samples, the estimated standard errors for mean differences of the non-linear regression model and the multiple-regression model were 0.066 and 0.074, respectively. In the jackknife samples, the standard

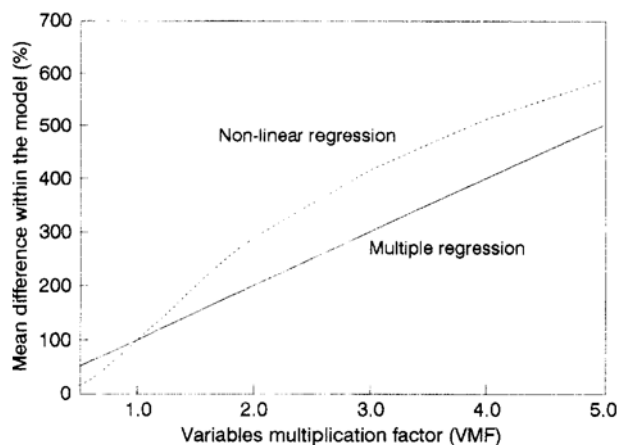


Figure 4. Changes of mean Pn difference (%) of *Q. mongolica* leaves as a consequence of changes of O_3 concentrations in the multiple-regression model and non-linear regression model.

errors were 0.009 and 0.009, respectively.

The percentile method used the 2.5 and 97.5 percentiles of bootstrap distribution as the limits of a 95% confidence interval, while the accelerated bootstrap method adjusted the percentile bootstrap for bias and skewness. The percentile bootstrap distribution of the mean difference in the non-linear regression model showed skewness to the right (Fig. 3). To correct for the skewed sample distribution, the accelerated bootstrap method for confidence interval of mean difference was used (Table 5). The accelerated confidence intervals in 1000 bootstrap replicates ranged from 0.212 to 0.477 in the non-linear regression model and from 0.665 to 0.954 in the multiple-regression model.

To simulate the effect of O_3 concentration on *Q. mongolica* leaves in urban areas the change of mean Pn difference was investigated, assigning the measured data of O_3 concentration as the 100% value and increasing variables multiplication factor (VMF) in O_3 concentration (Fig. 4). For each model, O_3 concentrations increased from 0.5 to 2.0 times.

In the non-linear regression model, the mean difference increased non-linearly as O_3 concentration increased; it was higher than the reference value when VMF was >1 and lower than the reference

value when VMF was < 1 . In the multiple-regression model, the mean Pn difference increased linearly as O_3 concentration increased; it was lower than the reference value when VMF was > 1.0 , but higher than the reference value when VMF was < 1 .

Discussion

The multiple-regression model was developed using climatic and anthropogenic factors affecting Pn and compared with the non-linear regression model used by Kim and Kim (1997). In the correlation analysis between Pn and the four air pollutants and/or two climatic factors, Pn was highly correlated with PPFD and T, but was negatively correlated only with O_3 concentrations. In multiple-regression, PPFD, T, SO_2 , and NO_2 variables had positive coefficients, but those of O_3 and TSP had negative. The same $\ln(PPFD)$, O_3 , T and SO_2 variables in the multiple-regression model were selected by forward selection and ridge regression. Photosynthetic capacity of *Q. mongolica* trees was primarily a function of PPFD, T, ambient O_3 and SO_2 concentration in Seoul, Korea.

It is suggested that a higher level of SO_2 concentration in winter may directly injure evergreen conifer species or may have an indirect effect through the soil on plants, whereas a lower level of SO_2 concentration in summer may not damage plants (Tomlinson II, 1983; Ptinz and Brandt, 1985). In this study, the highest SO_2 concentration was 19 ppb, which is probably too low to cause *Q. mongolica* leaves to damage. Also, the SO_2 variable in the multiple-regression model in Table 2 showed a positive effect on Pn, not negative. Thus, we used the model including $\ln(PPFD)$, O_3 , and T as regressors, removing the variable SO_2 (Table 4). The results are consistent with the previous work in the same forest stand (Kim and Kim, 1995, 1997), and support the hypothesis that short-term, low O_3 concentration exposures lead to photosynthesis or growth reduction of plant (Yang et al., 1983; Reich and Amundson 1984, 1985; Reich and Lassoie, 1985).

The non-linear regression model expressed as a type of power functions in previous works of Kim and Kim (1997) was compared with the selected multiple-regression model. The mean Pn difference in the non-linear regression model ($\mu_{nl} = 0.319 \mu\text{mol m}^{-2}\text{s}^{-1}$) was smaller than that of the multiple-regression model ($\mu_{lr} = 0.806 \mu\text{mol m}^{-2}\text{s}^{-1}$) for the original data. To assess the precision of the two mean Pn differences, the bootstrap and the jackknife procedures were used

(Lifson, 1987). When using the bootstrap and jackknife procedures in the two models, the biases of mean Pn difference and their estimated standard errors for each model were very small. This indicates that the number of observations for the two models was sufficient to estimate mean Pn difference and their estimated standard errors in each model. The percentile bootstrap distribution of the Pn difference in the non-linear regression model showed skewness to the right. The range of the bootstrap distribution of Pn difference between the two models did not overlap. This indicates that the two models may be used in qualitative or quantitative assessment of the effect of air pollutant on plant response.

To simulate the effect of O_3 concentration on *Q. mongolica* leaves in urban areas we increased O_3 concentration from 0.5 to 2.0 times. In the non-linear regression model, the mean difference increased non-linearly with an increase of O_3 concentration. In the multiple-regression model, the mean difference increased linearly with an increase of O_3 concentration as expected. The mean Pn difference in the non-linear regression model was 150% higher than that of the multiple-regression model when the variable multiplication factor (VMF) was more than 1.

The advantage of the multiple-regression model applied in this study was that it could verify the effects of air pollutants using the data of ecophysiological experiment in situ. However, several problems should be ensured before the start of an experiment. First, the PPFD as a dependent variable in field experiment is the most important limiting factor on Pn response. It should be considered that the measurements of Pn responses in situ are evenly made between light compensation point and the saturated PPFD according to the relationship between light and photosynthesis of each plant species. Second, the statistical assumptions should be considered. The collection of continuous hourly average data may cause the problem of autocorrelation of the data. In this study, in order to avoid such problem, measurements were made at monthly intervals during growth period and the data were selected at random. Third, the daily, seasonal and annual variations and distributions of air pollutants should be considered. Krupa and Kinkert (1987) pointed out that in the monitoring of hourly average ambient SO_2 concentrations, SO_2 concentrations were reported to be zero during approximately 90% of the monitored period. The daily and seasonal variations of daily 1-h maximum O_3 concentration were reported (Krupa et al., 1995; Kim and Kim, 1997). Therefore, if workers are to measure Pn of

leaves during periods of low concentrations of air pollutants, they cannot detect the effect of air pollutants. Fourth, a variation of leaf status such as leaf age, leaf location in the canopy or leaf water stress leads to no detection of the effects of air pollutant so that leaf status must be monitored during the measurement period. Thus, multiple-regression model is only applicable after the various conditions are suitably considered.

In conclusion, the results indicate that a multiple-regression model can be applicable to the qualitative or quantitative assessment of the effect of air pollutants on Pn response of plant leaves in situ. Also, the assessment of ecological effects using two kinds of numerical models, non-linear regression models and multiple-regression models, will have a degree of uncertainty associated with the measuring time of data used in the modelling, as well as with the numerical structure of the model.

Received November 30, 1998; accepted February 12, 1999.

LITERATURE CITED

- Brault S, Caswell H** (1993) Pod-specific demography of killer-whales (*Orcinus orca*). *Ecology* **74**: 1444-1454
- Cook ER, Johnson A** (1989) Climate change and forest decline: A review of the red spruce case. *Water Air and Soil Pollut* **48**: 127-140
- Efron B** (1987) Better bootstrap confidence intervals (with discussion). *J Amer Stat Assoc* **82**: 171-200
- Heck WW, Adams RM, Cure W, Heagle AS, Heggstad HE, Kohut RJ, Kress LW, Rawlings JO, Taylor OC** (1983) A reassessment of crop loss from ozone II. *Environ Sci Technol* **17**: 572A-581A
- Heck WW, Cure W, Rawlings JO, Zaragosa LF, Heagle AS, Heggstad ME, Kohut RJ, Kress LW, Temple PJ** (1984a) Assessing impacts of ozone on agricultural crops. I. Overview. *J Air Pollut Control Assoc* **34**: 729-735
- Heck WW, Cure W, Rawlings JO, Zaragosa LF, Heagle AS, Heggstad HE, Kohut RJ, Kress LW, Temple PJ** (1984b) Assessing impacts of ozone on agricultural crops. II. Crop yield functions and alternative exposure statistics. *J Air Pollut Control Assoc* **34**: 810-817
- Heck WW, Taylor OC, Adams R, Bingham G, Miller J, Pleston E, Weinstein L** (1982) Assessment of crop losses from ozone. *J Air Pollut Control Assoc* **32**: 353-361
- Hinrichsen D** (1987) The stands decline enigma: What underlies extensive dieback on two continents? *Bio-Science* **37**: 542-544C
- Hocking RR** (1976) The analysis and selection of variables in linear regression. *Biometrics* **32**: 1-51
- Hoerl AE, Kennard RW** (1970) Ridge regression: biased estimation for non-orthogonal problems. *Technometrics* **12**: 55-61
- Hong S-K, Nakagoshi N** (1998) Comparison of the initial demographics of pine and oak populations in rural pine forests in Korea and Japan. *J Plant Biol* **41**: 208-218
- Kim JW, Kim J-H** (1995) Responses in net photosynthetic rate of *Quercus mongolica* leaves to ozone. *Korean J Ecol* **18**: 265-273
- Kim JW, Kim J-H** (1997) Modelling the net photosynthetic rate of *Quercus mongolica* stands affected by ambient ozone. *Ecol Model* **97**: 167-177
- Krupa SV, Grunhage L, Jager H-J, Nosal M, Manning WJ, Legge AH, Hanewald K** (1995) Ambient ozone (O₃) adverse crop response: a unified view of cause and effect. *Environ Pollut* **87**: 119-126
- Krupa SV, Kickert RN** (1987) An analysis of numerical models of air-pollutant exposure and vegetation response. *Environ Pollut* **44**: 127-158
- Larson RI, Heck WW** (1976) An air quality data analysis system for interrelating effects, standards and needed source reductions. Part 3. Vegetation injury. *J Air Pollut Control Assoc* **26**: 325-333
- Long SP, Hallgren J-E** (1985) Measurement of CO₂ assimilation by plants in the field and the laboratory. In J Coombs, DO Hall, SP Long, JMO Scurlock, eds, *Techniques in Bioproductivity and Photosynthesis*, Ed 2. Pergamon Press, pp 62-94
- Manly BFJ** (1990) On the statistical analysis of niche data. *Can J Zool* **68**: 1420-1422
- Meldahl RS, Chappelka AH, Lockaby BG** (1992) Use of a non-linear model in examining growth responses of loblolly pine to ozone and acid precipitation. *Atmos Environ Part A- General topics* **26**: 279-286
- Meyers RH** (1990) *Classical and Modern Regression With Applications*. PWS-KENT Publishing Company, Boston
- Miller PR** (1989) Concept of forest decline in relation to western U.S. forests. In JJ MacKenzie, MT El-Ashry, eds, *Air Pollution's Toll on Forests and Crops*, Yale University Press, New Haven and London, pp 75-112
- Mohren GMJ, Jorritsma ITM, Vermetten AWM, Kropff MJ, Smeets WLM, Tikak A** (1992) Quantifying the direct effects of SO₂ and O₃ on stands growth. *For Ecol Manage* **51**: 137-150
- Moldau H, Suber J, Karolin A, Kallis A** (1991) CO₂ uptake and respiration losses in vegetative bean plants due to ozone absorption. *Photosynthetica* **25**: 341-349
- Mueller LD** (1979) A comparison of two methods for making statistical inferences on Nei's measure of genetic distance. *Biometrics* **35**: 757-763
- Potvin C, Roff DA** (1993) Distribution-free and robust statistical methods: Viable alternatives to parametric statistics? *Er ology* **74**: 1617-1628
- Prinz B, Brandt CJ** (1985) Effects of air pollution on vegetation. In HW Nornberg, eds, *Pollutants and Their Ecotoxicological Significance*, John & Sons Ltd, New York, pp 67-84
- Prinz B** (1987) Major hypotheses and factors: Causes of forest damage in Europe. *Environment* **29**: 11-15

- Reich PB, Ellsworth DS, Kloeppel BD, Fownes JH, Gower ST** (1990) Vertical variation in canopy structure and CO₂ exchange of oak-maple stands: Influence of ozone, nitrogen, and other factors on simulated canopy carbon gain. *Tree Physiol* **7**: 329-45
- Reich PB, Lassoie JP** (1985) Influence of low concentrations of ozone on growth, biomass partitioning and leaf senescence in young hybrid poplar plants. *Environ Pollut Ser A* **33**: 39-51
- Reich PB, Amundson RG** (1984) Low level O₃ and/or SO₂ exposure causes a linear decline in soybean yield. *Environ Pollut Ser A* **34**: 345-355
- Reich PB, Amundson RG** (1985) Ambient levels of ozone reduce net photosynthesis in tree crop species. *Science* **1230**: 566-570
- Rhyu TC, Kim J-H** (1994a) Growth response to acid rain, Mg deficiency and Al surplus, and amelioration of Al toxicity by humic substances in pitch pine seedlings. *J Plant Biol* **37**: 301-308
- Rhyu TC, Kim J-H** (1994b) Water deficit of pitch pines caused by superficial rooting and air pollutants in Seoul and its vicinity. *J Plant Biol* **37**: 309-316
- SAS** (1993) SAS User's Guide, Statistics, Version 6. SAS Institute, Inc., Cary, NC
- Shapiro SS, Wilk MB** (1965) An analysis of variance test for normality (complete samples). *Biometrika* **52**: 591-611
- Smith EP** (1985) Estimating the reliability of diet overlap measures. *Environ Biol Fishes* **13**: 125-38
- Smith EP, Genter RB, Cairns J** (1986) Confidence intervals for the similarity between algal communities. *Hydrobiologia* **139**: 237-245
- Tomlinson II GH** (1983) Air pollutants and forest decline. *Environ Sci Technol* **17**: 246A-55A
- Yang Y-S, Skelly JM, Chevone BI, Bilch JB** (1983) Effects of long-term ozone exposure on photosynthesis and dark respiration of eastern white pine. *Environ Sci Technol* **17**: 371-373