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Relative Importance of Bottom-up vs. Top-down Controls on Size-structured Phytoplankton Dynamics in a Freshwater Ecosystem: II. Investigation of Controlling Factors using Statistical Modeling Analysis

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Relative importance between bottom-up and top-down controls on phytoplankton dynamics was investigated in the Juam Reservoir, Chonnam based on the results from statistical analyses including regression and artificial neural network (ANN) modeling. Effects of nutrients on size-structured phytoplankton dynamics were explored by simple linear regression analysis and relative importance between bottom-up and top-down controls was estimated based on results from the artificial neural network analyses. Although there is a limitation in determining direct grazing effects since chlorophyll *a* : pheopigments ratios, indirect index for grazing activity rather than grazing rates or herbivores biomass were used, the results from regression analysis showed that nutrients especially orthophosphates were positively correlated with the phytoplankton biomass and chlorophyll *a* : pheopigments ratios were also positively correlated with the phytoplankton biomass at lower coefficient of determination (r^2) compared to orthophosphates. The simulation results from ANN suggested that the bottom-up mechanisms including water temperature and availability of nutrients, especially orthophosphates were more important than top-down mechanisms such as grazing in the phytoplankton dynamics.

Key words : artificial neural networks, controlling factors, nutrients, Lake Juam, phytoplankton

INTRODUCTION

Understanding the dynamics of phytoplankton is important since as primary producers they are the main source of carbon and nutrients (e.g. N, P) in a food web (Kemp and Boynton, 1981; Boynton *et al*., 1982; Coffin and Sharp, 1987; Sundbaeck *et al*., 1990). Phytoplankton affect water quality, especially dissolved oxygen by photosynthesis and respiration and can serve as substrates for microbial decomposition resulting

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in oxygen depletion when their ungrazed biomass has accumulated (Malone *et al*., 1986; Sundbaeck *et al*., 1990).

Two concepts are generally accepted as the major mechanisms governing phytoplankton dynamics in aquatic systems. One is bottom-up control such as nutrient supply related to physical-chemical variations (i.e. abiotic mechanisms) and the other is top-down control (i.e. biotic, trophic interactions). There has been continuing debate regarding the relative importance of bottom-up vs. top-down controls and established concepts of resource competition (Tilman, 1982) and trophic cascade (Carpenter *et al*., 1985) or the trophic biomanipulation theory (Shapiro and Wright, 1984). It is generally accepted that the relative importance of bottom-up vs. top-down regulations of phytoplankton structure is scale-dependent; the structure is determined neither entirely by resources competition nor trophic cascade over time scales of interest (Hansson, 1992).

Artificial neural networks (ANNs), which are composed of simple elements operating in parallel, can be trained to solve many complex problems in almost all fields of science and technology (Karul *et al*., 2000; Gevrey *et al*., 2003). Three layer backpropagation feedforward neural network with a sigmoid transfer function at the input layer can approximate any function that has finite number of discontinuities (Priyantha *et al*., 1997; Olden, 2000; Wilson and Recknagel, 2001; Lee *et al*., 2003; Jeong *et al*., 2003). In recent years, neural networks were used in the fields of limnology and phytoplankton dynamics (Olden, 2000; Jeong *et al*., 2001; Scardi, 2001; Lee *et al*., 2003). Neural networks are ideal to estimate this nonlinear behavior of chlorophyll *a* as well as major controlling factor between bottom-up vs. top-down controls of phytoplankton dynamics since phytoplankton dynamics are complex interacting with environmental factors (nutrients, light, hydrodynamics) and herbivores.

In the companion paper (Sin and Kim, 2003), temporal and spatial variations of size-structured phytoplankton and physical properties were reported and the principal goals of this study were to examine the relationship between phytoplankton size classes and various chemical properties and then determine the relative importance between bottom-up and top-down mechanisms controlling phytoplankton dynamics in the Lake Juam by statistical analyses including regression and artificial neural network analyses.

MATERIALS AND METHODS

Study site and nutrient measurements

Lake Juam is composed of the Bosung River, a subriver of the Sumjin River and general characteristics of the Lake Juam and measurements of chlorophyll *a* and physical properties were described in a companion paper (Sin and Kim, 2003). In addition to the physical properties reported by Sin and Kim (2003), nutrient concentrations including dissolved nitrogen (DN) dissolved phosphorous (DP), total nitrogen (TN), total phosphorous (TP), ammonium (NH_4^+), nitrate (NO_3^-), phosphate (PO_4^{3-}) were measured in the Lake Juam. Figure 1 shows sampling stations to collect data employed in this study. For nutrient measurements samples were filtered using GF/F (0.7 μm pore size) and stored at refrigerator (in 250 mL PE bottles) until analyzed as discussed in Parsons *et al*. (Parsons *et al*., 1984). After measurement of chlorophyll *a* using a Turner Designs-10-AU Fluorometer, two drops of HCl (2N) were added and the extracts re-read for determination of pheopigments following acidification. Grazers

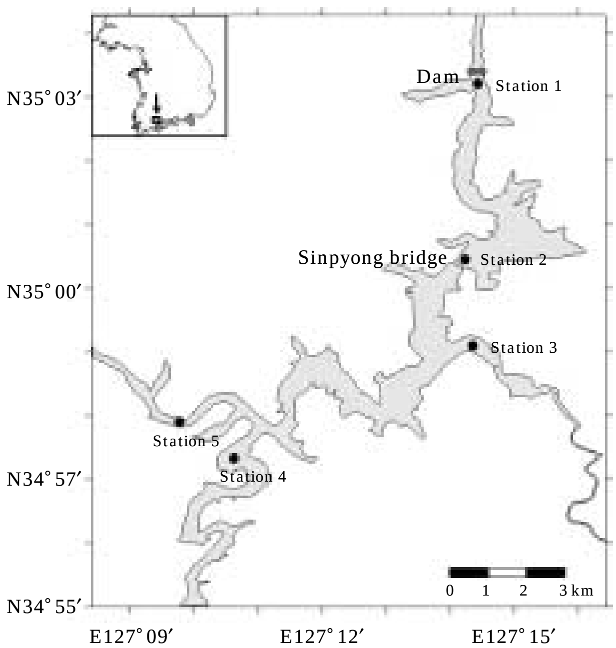

Fig. 1. Sampling stations in the lower (Stations 1, 2, 3) and upper (Stations 4, 5) regions of Lake Juam.

convert chlorophyll *a* to pheopigments, which are released as egested fecal material. The ratio of chlorophyll *a* and pheopigments, determined by the ratios of fluorescence before and after acidification is an indirect measure of grazing activity (e.g. Welschmeyer and Lorenzen, 1985); the lower the ratio, the higher the grazing rates. Suspended pheopigments can also be produced within phytoplankton cells during senescence as a result of poor growth environments or prolonged exposure to the dark (Yentsch, 1967; Daley and Brown, 1973).

Simple linear regression analysis

Using a simple linear regression, the relationships were explored between the chlorophyll *a* concentrations of various phytoplankton size classes and various chemical properties of the Lake Juam, specifically dissolved nitrogen (DN), dissolved phosphorus (DP), total nitrogen (TN), total phosphorus (TP), ammonium, nitrate, orthophosphate, DN : DP, TN : TP, and DIN ($NH_4^+ + NO_3^-$) : DIP (PO_4^{3-}) molar ratios as well as chlorophyll *a* : pheopigments ratio. Phytoplankton size classes included three size classes: micro-size (> 20 μm), nano-size (3-20 μm) and pico-size (< 3 μm).

Framework of artificial neural network

The used network consists of three layers: input layer of 17 neurons, hidden layer of five neurons, output layer of one neuron which is the output variable (Fig. 2). There are connection weights between input and hidden layers, hidden and output layers. The network was trained using an error backpropagation training algorithm. This algorithm adjusts the connection weights according to the backpropagated error computed between the observed and the estimated results. This procedure minimizes the error between the desired and the predicted outputs (Gevrey *et al*., 2003; Lee *et al*., 2003).

The input data were transformed by Weibull distribution probability function (equation 1) since the variations of the field data are high and stochastic, and ranges of the input data are different between variables (c.f. Martz and Walker, 1982; Mann *et al*., 1997). After the transformation, the data sets have been rescaled into a [0,1] interval before training the neural networks,

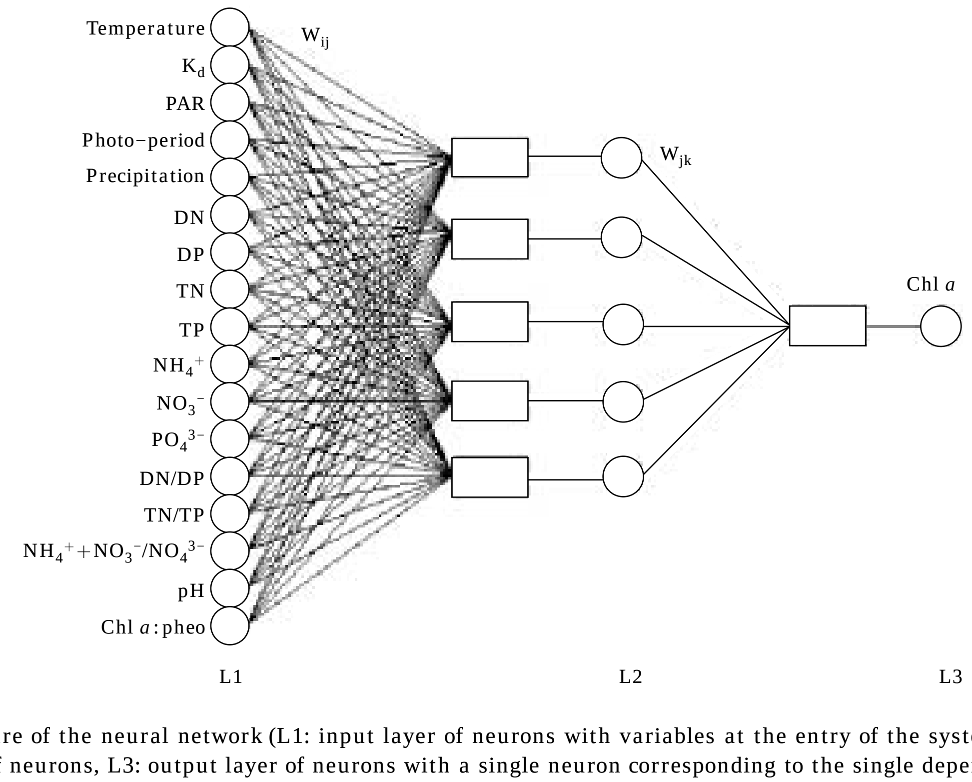

Fig. 2. Structure of the neural network (L1: input layer of neurons with variables at the entry of the system, L2: hidden layer of neurons, L3: output layer of neurons with a single neuron corresponding to the single dependent variable, W_{ij} and W_{jk} : the weights between hidden and input layer, and between output and hidden layer).

whereas neural network output has always been scaled back to its original units. To introduce nonlinearity into a system the sigmoid function is adopted as the activation functions that transfers the summed inputs to the output layer (c.f. Scardi, 2001).

$$F(t) = 1 - \exp\left[-\left(\frac{t}{\alpha}\right)\right]^{\beta} \quad (1)$$

where, α = Measuring Parameter, β = Shape Parameter

To investigate phytoplankton dynamics chemical, physical and biological parameters were periodically measured in the Juam reservoir and the parameters were considered as input neurons for ANN modeling processes including water temperature, light attenuation coefficients (K_d), PAR at 1.1 m water depth, photo-period, precipitation, dissolved nitrogen (DN) dissolved phosphorous (DP), total nitrogen (TN), total phosphorous (TP), ammonium, nitrate, phosphate, pH, DN : DP, TN : TP, $NH_4^+ + NO_3^-/PO_4^{3-}$(DIN/DIP), and chlorophyll *a* : pheopigments ratio.

Chlorophyll *a* was used as the primary target output of the training sessions. Chlorophyll *a* which represent phytoplankton biomass in ecosystems was output neurons in output layer of ANN modeling processes.

RESULTS

Simple linear regression analysis

Table 1 shows results (r^2) of linear regression analyses of relationships between the chlorophyll *a* concentrations of phytoplankton size classes and various chemical properties of the Lake Juam, specifically dissolved nitrogen (DN), dissolved phosphorus (DP), total nitrogen (TN), total phosphorus (TP), ammonium, nitrate, orthophosphate, DN : DP, TN : TP, and DIN : DIP ratios as well as chlorophyll *a* : pheopigments ratio. Phytoplankton size classes generally showed positive relationship with DN whereas size classes had negative relationships with DP. TP was also positively correlated with (α = 0.05) chlorophyll *a* concentrations of the size classes except nano-size class at Station 3. Nitrate was negatively correlated with chlorophyll *a* concentrations of the size classes whereas the opposite relationship was observed for orthophosphate. DN/DP ratios were generally positively correlated with chlorophyll *a* concentrations of size classes except nano-size class whereas TN : TP ratios were negatively correlated with chlorophyll *a* concentrations except nano-sized chlorophyll *a* concentrations. Nano-sized chlorophyll *a* concentrations were significantly positively correlated with DIN : DIP ratios (α = 0.05) whereas other sized chlorophyll *a* concentrations were generally negatively correlated. Chlorophyll *a* : pheopigments ratios were positively correlated with chlorophyll *a* concentrations of size classes.

Artificial neural network analysis

After the training of 10,000 iterations, the mean square error decreased lower than 0.07 with 5

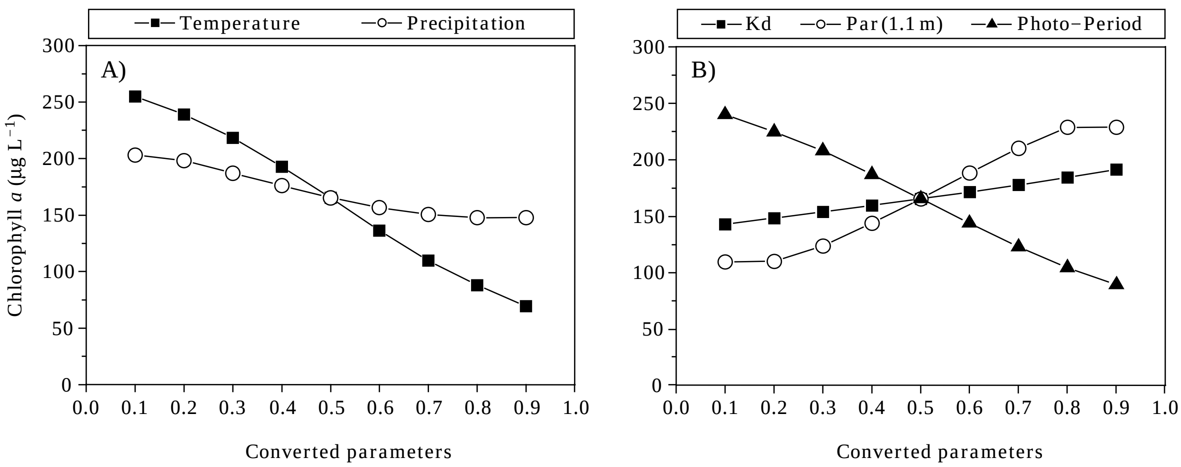

Fig. 3. Response of phytoplankton biomass (chlorophyll *a*) to changes of : (A) temperature (°C) and precipitation (mm); (B) light attenuation coefficients (m^{-1}) and photo-period (h) in the artificial neural network model for the Lake Juam.

hidden nodes. Results from Fig. 3 to Fig. 5 represent the variation of chlorophyll *a* in response to converted input data using Weibull distribution probability. Chlorophyll *a* concentrations were decreased as water temperature and precipitation increased (Fig. 3A). Negative relationship was also observed between chlorophyll *a* concentrations and photo-period whereas positive relationship observed with light attenuation coefficients and PAR at 1.1 m water depth (Fig. 3B). Chlorophyll *a* concentrations were increased as DN and DP increased (Fig. 4B). Negative relationship was observed between chlorophyll *a* concentrations and TN whereas positive relationship observed with TP (Fig. 4C). Chlorophyll *a* concentrations were decreased as dissolved inorganic nitrogens such as ammonium (NH_4^+) and nitrate (NO_3^-) were increased but phytoplankton biomass was increased as orthophosphate (PO_4^{3-}) concentrations increased (Fig. 4A). Chlorophyll *a* concentrations were decreased as ratios of TN : TP and DIN : DIP increased (Fig. 4D). Chlorophyll *a* concentrations were increased as chlorophyll *a* : pheopigments ratios increased but the concentrations did not respond to increase of pH (Fig. 5).

The simulation results suggested that water temperature, photo-period, nitrate and total nitrogen (TN) are the major factors affecting phytoplankton biomass negatively whereas PAR (1.1

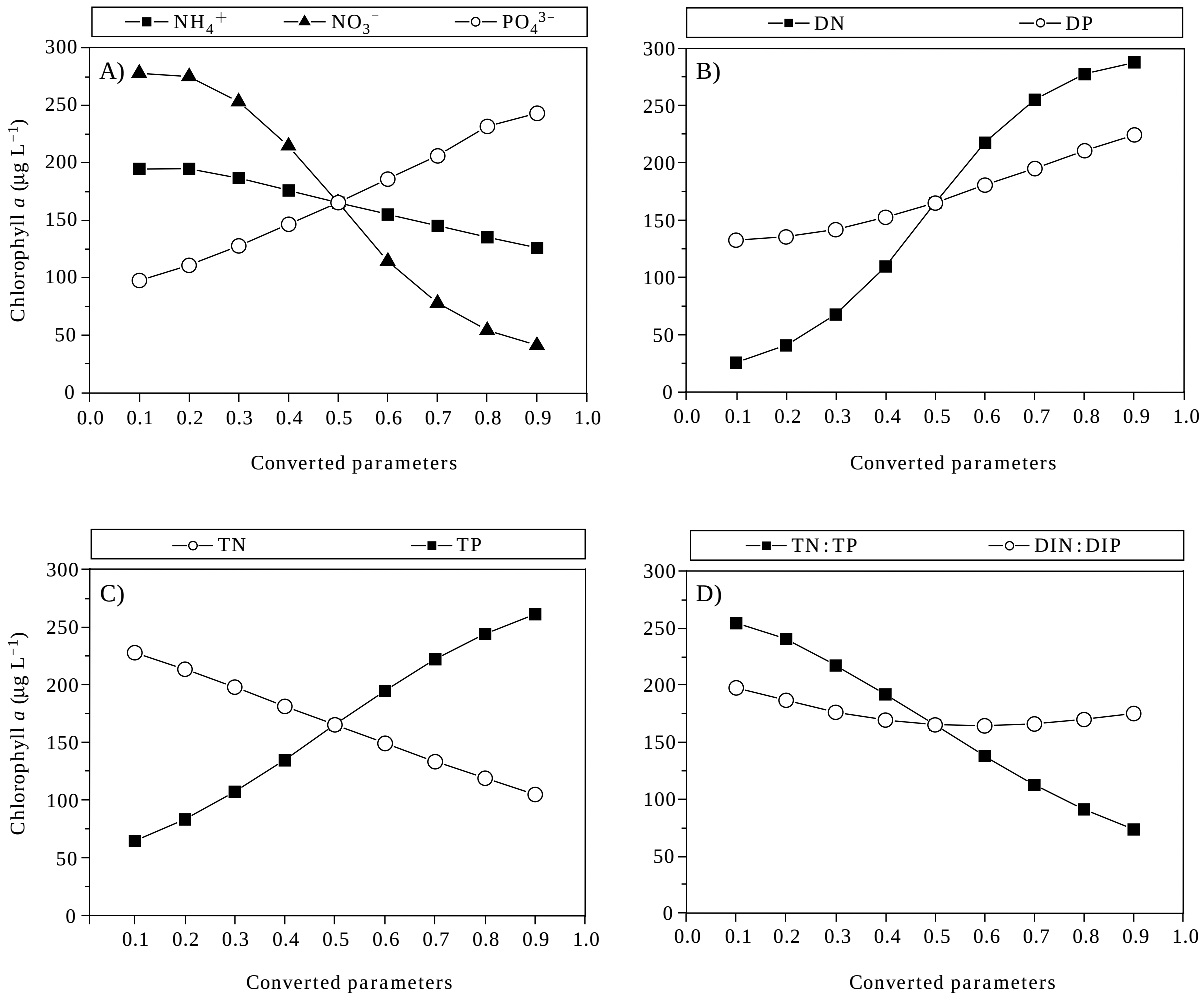

Fig. 4. Response of phytoplankton biomass (chlorophyll *a*) to changes of : (A) NH_4^+, NO_3^- and PO_4^{3-} (μM); (B) dissolved nitrogen (DN, μM) and dissolved phosphorus (DP, μM); (C) total nitrogen (TN, μM) and total phosphorus (TP, μM); (D) TN : TP and DIN ($NH_4^+ + NO_3^-$) : DIP (PO_4^{3-}) molar ratios in the artificial neural network model for the Lake Juam.

Table 1. Results (r^2) of linear regression analyses of surface chlorophyll *a* (μg L^{-1}) vs. dissolved nitrogen (DN, μM), dissolved phosphorus (DP, μM), total nitrogen (TN, μM), total phosphorus (TP, μM), nutrients (NH_4^+, NO_3^- and PO_4^{3-}), molar ratios of DN : DP, TN : TP and DIN : DIP, and chlorophyll *a* : pheopigments ratios during the sampling period. r^2 values less than 0.2 were omitted and denoted by−. Negative values denote negative relationship

		DN	DP	TN	TP	NH_4^+	NO_3^-	PO_4^{3-}	DN/DP	TN/TP	DIN/DIP	chl *a* : pheo
Whole chlorophyll *a*	Station 1	−	−	−	0.81[b]	−	−	−	−	−0.32	−	−
	Station 2	−	−0.58[a]	−	0.22	−	−	0.70[b]	0.35	−0.23	−0.41	0.45
	Station 3	−	−	−	−	−	−	0.47[a]	−	−	−0.29	0.45[a]
	Station 4	0.28	−	0.34	0.24	−	0.30	0.29	−	−	−	−
	Station 5	−	−	−	−	−	−0.53[a]	−	−	−	−	0.51[a]
Micro-size class	Station 1	−	−	−	0.81[b]	−	−	−	−	−0.31	−	−
	Station 2	−	−0.58[a]	−	0.21	−	−	0.69[b]	0.34	−0.22	−0.41	−
	Station 3	−	−	−	−	−0.20	−	0.44[a]	−	−	−0.28	0.36
	Station 4	0.39	−	0.50	0.37	−	0.32	0.39	−	−	−	−
	Station 5	−	−	−	−	−	−0.51[a]	−	−	−	−	0.32
Nano-size class	Station 1	−	0.22	−	−	−	−	−	−0.38	−	0.50[a]	−
	Station 2	−	−	−	−	−	0.24	−	−	−	−	−
	Station 3	−	−	−	−0.53[b]	−	−	0.38	−	0.52[b]	−	−
	Station 4	−	−	−	−	−	−	−	−	−	−	−
	Station 5	−0.40	−	−	−	−	−0.87[b]	−0.30	−0.37	−0.20	−0.23	0.36
Pico-size class	Station 1	0.21	−	−	0.35	−	−	−	0.20	−	−	0.65[b]
	Station 2	0.27	−0.54[a]	0.21	0.46	0.26	−	0.85[b]	0.63[a]	−	−0.24	0.22
	Station 3	−	−	−	−	−	−	0.74[b]	−	−	−	−
	Station 4	−	−	−	0.48	−	−	−	−	−0.32	−	−
	Station 5	−	−	−	−0.23	−	−	−	0.40	0.40	0.39	0.41

[a]$P < 0.1$, [b]$P < 0.05$

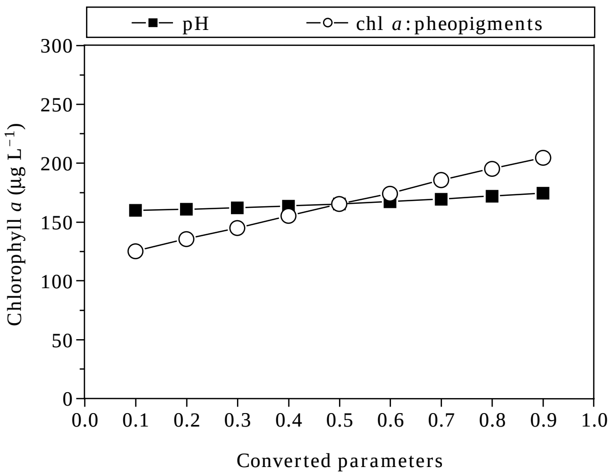

Fig. 5. Response of phytoplankton biomass (chlorophyll *a*) to changes of pH and chlorophyll *a* : pheopigments ratio in the artificial neural network model for the Lake Juam.

m), orthophosphate (PO_4^{3-}), DP and TP are the major factors affecting positively. The chlorophyll *a* : pheopigments ratios, indirect index for grazing activity of grazers, affected phytoplankton biomass but the relative importance was not high compared with other factors including physical and chemical properties.

DISCUSSION

In the companion paper (Sin and Kim, 2003), biomass of larger phytoplankton (micro-sized) was high in the lower region of the Lake Juam and phytoplankton blooms were mainly predominated by large cells i.e. micro-size class throughout the sampling period. The results from regression analyses on chemical parameters (Table 1) show that correlationship between micro-sized phytoplankton and various parameters is generally similar to relationship between total chlorophyll *a* and chemical properties. Phytoplankton size classes were significantly and negatively correlated with nitrogen nutrients including ammonium and nitrate but positively correlated with orthophosphate. This results suggest that phytoplankton growth is limited by P and supply of dissolved inorganic phosphorus contribute to phytoplankton blooms in the Lake Juam. The potential P limitation was also reported based on long-term data analyses for the Lake Juam (Chang *et al*., 2004). DIN : DIP and TN : TP molar ratios were also higher than 16 : 1 in this study (data not shown).

Artificial neural networks (ANNs) has been used in order to predict multivariate or non-linear data. Applications of ANNs in ecological and environmental science have been reported since the beginning of the 1990s (Barciela *et al*., 1999; Lee *et al*., 2003). The advantages of ANNs are: (i) they can provide quick response and hence are well-suited for real time operation; and (ii) most importantly ANNs can model dynamic, non-linear, especially when physical/chemical/biological processes are interacting complicate. Neural networks are powerful tools for studying phytoplankton dynamics and the neural networks were employed to predict phytoplankton dynamics in Nakdong River (Jeong *et al*., 2001). Algal bloom dynamics of the coastal water of Hong Kong were also investigated by using backpropagation learning algorithm (Lee *et al*., 2003). In this study, the ANNs were used to determine relative importance between bottom-up and top-down controls in phytoplankton dynamics in the Lake Juam. Results from the ANNs simulation (Figs. 3-5) showed that phytoplankton biomass may be controlled by water temperature and this scenario is supported by the negative relationship between micro-sized chlorophyll *a*, dominant size class during the sampling period, and water temperature (Sin and Kim, 2003). Nitrates and orthophosphates were also correlated with simulated phytoplankton biomass but the relationships were reversed (Fig. 4A). Results from regression analyses on the nutrients vs. various sized-chlorophyll *a* showed the similar relationships (Table 1). N : P ratios of ambient nutrient concentrations in this study were much higher than 16 : 1 suggesting that phytoplankton growth may be limited by P. The positive relationships of orthophosphates with chlorophyll *a* concentrations and the high N : P ratios suggest that orthophosphates are more important nutrients controlling the phytoplankton biomass in the Lake Juam. Various sized-chlorophyll *a* concentrations were positively correlated with ratios of chlorophyll *a* : pheopigments (indirect index of grazing activity by grazers) suggesting that phytoplankton biomass is controlled by grazing pressure of grazers in the Lake Juam (Table 1). Simulated phytoplankton biomass in the ANNs modeling also showed a positive relationship with the ratios of chlorophyll *a* : pheopigments but the sensitivity of chlorophyll *a* to the changes of chlorophyll *a* : pheopigments ratio was low compared with other parameters such as temperature and nutrients. Although more complete investigations including direct grazing effects and other sink processes are required, these results suggest that bottom-up mechanisms including water temperature and nutrient availability are relatively important compared to top-down mechanisms such as biological interaction (i.e. grazing) in the Lake Juam.

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<국문적요>

담수성 식물플랑크톤의 크기별 동태에 대한 상향식, 하향식 조절간의 상대적 중요도 조사: II. 통계 모델링 분석을 이용한 조절인자 분석

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전남 주암호에서의 식물플랑크톤 동태를 파악하기 위해 2003년 2월부터 10월까지 식물플랑크톤 생물량(클로로필 *a*)의 크기별 시 · 공간적 변동과 제반 환경요인에 대해 조사하였다. 본 논문에서는 주암호와 같은 담수호에서 식물플랑크톤의 크기 구조가 계절적, 공간적으로 나타나는 변동에 대한 영양염들의 영향을 회귀분석을 통해 파악하고자 하였다. 또한 인공지능망을 이용하여 전체 식물플랑크톤의 생물량(클로로필 *a*)에 대한 상향식, 하향식 조절인자들에 대한 상대적인 중요도를 정량적으로 파악하고자 하였다. 비록 동물플랑크톤 포식압을 나타내는 포식율이나 동물플랑크톤 생체량 대신 포식압의 간접 지수인 chlorophyll *a* : pheopigments ratio를 활용하였지만 회귀분석결과, 영양염 특히 인산염과 식물플랑크톤의 생물량이 양의 상관관계를 갖는 것으로 나타났고 chlorophyll *a* : pheopigments ratio도 결정계수가 다소 낮기는 하지만 양의 상관관계를 보여 주었다. 인공지능망 시뮬레이션 결과에서는 주암호 식물플랑크톤의 생물량은 수온, 영양염 특히 인산염과 같은 상향식 조절이 우세한 것으로 나타났다.