Photosynthetic traits of *Carex cinerascens* in flooded and nonflooded conditions

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Abstract

Gas exchange of *Carex cinerascens* was carried out in Swan Islet Wetland Reserve (29°48′ N, 112°33′ E). The diurnal photosynthetic course of *C. cinerascens* in the flooded and the nonflooded conditions were analyzed through the radial basis function (RBF) neural network approach to evaluate the influences of environmental variables on the photosynthetic activity. The inhibition of photosynthesis induced by soil flooding can be attributed to the reduced stomatal conductance (g_s), the deficiency of Rubisco regeneration and decreased chlorophyll (Chl) content. As revealed by analysis of artificial neural network (ANN) models, g_s was the dominant factor in determining the photosynthesis response. Weighting analysis showed that the effect of water pressure deficit (VPD) > air temperature (T) > CO_2 concentration (C_a) > air humidity (RH) > photosynthetical photon flux density (PPFD) for the nonflooded model, whereas for the flooded model, the factors were ranked in the order VPD > C_a > RH > PPFD > T. The different photosynthetic response of *C. cinerascens* found between the nonflooded and flooded conditions would be useful to evaluate the flood tolerance at plant species level.

Additional key words: ANN; *Carex cinerascens*; photosynthesis.

Introduction

Periodical soil floodings occurring in wetland have significant implications for wetland plants (Ponnamperuma 1984). Soil flooding causes morphological and physiological changes in many species (Brown and Pezeshki 2000, Mommer *et al.* 2006). Soil flooding reduces photosynthetic rates in many wetland plants (Pezeshki 2001). The decline in photosynthesis under flooding has been attributed to stomatal closure (Bradford 1983) and

some metabolic inhibition (Pezeshki *et al.* 1993, Liao and Lin 1994, Mishra *et al.* 2008). Production of ethylene (Pallas and Kays 1982, Taylor and Gunderson 1988), decrease of Chl content (Bradford 1983, McKevlin *et al.* 1995) and ribulose-1,5-biosphosphate carboxylase/oxygenase (Rubisco) activity (Pezeshki 1994) have been reported playing an important role in the photosynthetic decrease after soil flooding.

Carex cinerascens Kükenth. is widely distributed in the catchment area of the Yangtse River, and it can be used in wetland restoration. It is competitive in riparian areas and wetland. *C. cinerascens* has been found to tolerate extensive flooding, but little information exists on this species´ tolerance to long-term soil flooding in this region (Li *et al.* 2007). Investigation about the effects of long-term soil flooding on photosynthesis of *C. cinerascens* would be meaningful to characterize the probable further performance of the species in wetland restoration.

Studies showed that photosynthetic response of plants under specific stress might show an altered sensitivity to environmental factors (Poorter 1998). Balls *et al.* (1996) found that water-pressure deficit (VPD) and photosynthetically active radiation (PAR) had a stronger influence on the response to ozone than did temperature by the analysis of the weightings of factors through an artificial neural network (ANN) model. Artificial neural network (ANN) is a mathematical structure designed to mimic the information-processing functions of a network of neurons in the brain (Wasserman 1989). Neural network techniques have been widely utilized in the field of

environmental biology (Huntingford and Cox 1997, Jeong *et al.* 2001, Melesse and Hanley 2005). In our study, we hypothesized that different photosynthetic response traits to soil flooding, evaluation of the details of the differences about the photosynthesis response to natural environmental factors and plant-related factors between flooded and nonflooded conditions can give us further information about the photosynthetic characteristics of *C. cinerascens*. As a complement to field studies, mathematical models can be used as tools to avoid losing some information by observations. The ANN models are data-oriented methods with which we can use the full meaning of observed data. In addition, owing to the great amount of data collected in our studies, the complexity of the interactions between environmental variables and soil flooding in determining photosynthetic response in *C. cinerascens* makes it necessary to use the ANN models. In this paper, the radial basis function (RBF) neural network was applied to model of the photosynthetic response to biotic and abiotic factors. The objective of the present study was to investigate the influence of long-term soil flooding on the photosynthetic response of *C. cinerascens*.

Materials and methods

Study area: Experiments were carried out in the Swan Islet Wetland Reserve (29°48′ N, 112°33′ E), from 15 July to 17 September 2005. In the marsh, moderate slopes are found commonly due to frequent inundation. The experiment was performed in a sloping meadow (20 × 20 m, with a slope of 5°) where the soil composition was 33%, 50%, and 17% of sand, silt and clay, respectively, and pH was 7.2 (Li *et al.* 2007). Two kinds of sample plots were selected: in the nonflooded treatment, the water level was 20 cm below the soil surface and in the flooded treatment the water level was 20 cm above the soil surface. Six randomly selected plants of *C. cinerascens* were measured in each treatment.

Leaf gas-exchange measurement: 0, 30, and 60 days after flooding, the photosynthesis of fourth expanded leaves was measured between 12:00 and 13:00, in natural conditions (irradiance 1,500–1,800 μmol m^{-2} s^{-1}), using a *Licor 6400* Portable Photosynthesis System (*Li-COR Inc.*, Lincoln, NE, USA). The diurnal trend of the photosynthetic parameters was measured from 06:00 to 18:00 at intervals of two hours, and 48 measures per interval were taken. Net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), transpiration rate (E), photosynthetic photon flux density (PPFD), air temperature (T), leaf temperature (T_l), water-pressure deficit (VPD), air humidity (RH), and CO_2 concentration (C_a) were recorded simultaneously. Water-use efficiency (WUE) was calculated as the quotient of the photosynthetic rate over the transpiration rate. Photosynthetic light (P/I)- and CO_2-responses (P/C_i) were

measured at 25°C air temperature by an internal red and blue radiation source (*LI6400-02*). Ten irradiance levels (0, 20, 50, 100, 200, 500, 1,000; 1,500; and 2,000 μmol m^{-2} s^{-1}) were used. C_a entering into the chamber was regulated at 370 μmol mol^{-1} through a CO_2 mixer. The flux of air entering into the cuvette was settled at 400 μmol s^{-1}. Leaves were acclimated to each PPFD for at least 4 min, then steady-state gas-exchange properties were observed and logged, and subsequently the PPFD in the cuvette was changed. Light-response curves were plotted using the mean values of P_N measured at each PPFD. Light-response data were fitted to a model of non-rectangular hyperbola (Marshall and Biscoe 1980) to estimate the apparent quantum efficiency (AQY), light compensation point (Lc), light saturation point (Ls) and dark-respiration rate (R_D). The photosynthetic CO_2-response was measured at 1,500 μmol m^{-2} s^{-1} PPFD and different cuvette CO_2 concentrations obtained using the *LI-6400* CO_2 mixer. The maximum rate of carboxylation (V_{cmax}) and the light-saturated rate of electron transport (J_{max}), day respiration (R_{day}), and CO_2 compensation point (Γ) were estimated using the mechanistic model proposed by Farquhar *et al.* (1980). The carboxylation efficiency (CE) was calculated as the initial slope of the CO_2-response curve.

To investigate the *C. cinerascens* P_N response to biotic and abiotic factors in flooded and nonflooded conditions, the measured data (diurnal course of photosynthesis after 30 and 60 days of soil flooding) were divided into two dataset, flooded dataset for the flooded condition and nonflooded dataset for the nonflooded condition.

Table 1. Photosynthetic parameters and environmental factors.

Variables	Whole dataset		Nonflooded dataset		Flooded dataset	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
P_N [μmol m^{-2} s^{-1}]	9.63	5.10	10.37	5.11	8.87	4.98
g_s [mol m^{-2} s^{-1}]	0.246	0.099	0.248	0.115	0.243	0.077
C_i [μmol mol^{-1}]	263.9	38.9	257.0	37.5	271.4	39.1
E [mmol m^{-2} s^{-1}]	4.61	1.95	4.66	1.99	4.56	1.91
VPD [kPa]	2.06	0.673	2.11	0.673	2.0124	0.671
T [°C]	32.8	4.38	32.9	4.15	32.7	4.63
T_l [°C]	32.8	4.26	33.1	4.17	32.6	4.34
C_a [μmol mol^{-1}]	355.9	14.9	356.1	15.7	355.8	13.9
RH [%]	50.18	9.35	49.97	8.98	50.40	9.76
PPFD [μmol m^{-2} s^{-1}]	1,095.4	536.1	1,065.9	535.9	1,127.5	535.4

Each example includes the values of the nine environmental variables and the corresponding P_N statistical characteristics of the measured data were listed in Table 1.

Chl fluorescence measurement: Five fully-expanded leaves were selected for Chl fluorescence investigation using a *LI6400-40* fluorometer. Minimum fluorescence of dark-adapted state (F_o) and maximum fluorescence of dark-adapted state (F_m) were determined with a modulated irradiation (<1 μmol m^{-2} s^{-1}) shortly after keeping the leaves in the dark for 20 min. A saturating pulse of 7,000 μmol m^{-2} s^{-1} was applied for measurements of F_m. The leaves were continuously illuminated with actinic light at the intensity of 300 μmol m^{-2} s^{-1}, maximum fluorescence (F_m') and steady-state fluorescence (F_s) were measured by applying a second saturating pulse. Minimum fluorescence (F_o') were measured after far-red illumination of the previously exposed leaves. Using the fluorescence parameters determined above, the following parameters were calculated: maximum quantum yield of PSII [$F_v/F_m = (F_m-F_o)/F_m$], effective quantum yield of PSII (Φ_{PSII}) [$\Phi_{PSII} = (F_m' - F_s)/F_m'$], electron transport rate (ETR) [ETR $= \Phi_{PSII} \times$ PFD $\times 0.5 \times 0.84$], photochemical quenching (q_P) [$q_P = (F_m' - F_s)/(F_m' - F_o')$], and non-photochemical quenching coefficient (q_N) [$q_N = 1 - (F_m' - F_o')/(F_m - F_o)$] (Genty *et al.* 1989; Schreiber *et al.* 1994).

Chl content: Leaves used for photosynthetic measurements were collected and Chl concentration was determined by the method of Lichtenthaler (1987).

Artificial neural network model analysis: Diurnal course data in the experiments were used to train back propagation neural networks using *Matlab 7.0* (*MathWorks, Inc.,* USA). The RBF neural network, a type of feedforward neural network that learns using a supervised training technique, was selected to model the relationship between P_N and variables due to its higher accuracy in approximating continuous function mapping (Park and Sandberg 1991, Bianchini *et al.* 1995). The RBF neural networks were trained on the experimental data. Two models were created using g_s, C_i, E, VPD, T,

T_l, C_a, RH and PPFD as inputs, and P_N was the output. Training was carried out for 5,000 iterations. The nonflooded model and the flooded network reached a root mean squared (RMS) error of 0.0055 and 0.0061 on the training dataset by the end of the training period. This parameter indicates the effectiveness of the network; smaller RMS values meant the higher accuracy of the models. After training work, the performance of the RBF models were evaluated by the correlation coefficient and absolute errors between the predicted and observed values. Finally, two models with best performance were identified for the nonflooded dataset and flooded dataset, respectively. The models were then used to predict the output for a range of inputs.

Using the trained RBF networks models, sensitivity analysis was implemented on flooded and nonflooded dataset. To compute the sensitivity of P_N to one specific variable, two simulations were made. In the first simulation, the trained RBF network was fed with original input vectors in the testing subset and the output values represented the predictions with nondisturbed inputs. In the second simulation, the components corresponding with the specific variable in the input vectors were disturbed by +1 SD (the standard deviation of the specific variable computed using the whole data) and the network outputs represented the predictions with disturbed inputs by +1 SD of the specific variable. Subtracting the nondisturbed predictions from the disturbed outputs, the sensitivity of photosynthesis to +1 SD change of the specific variable on every data example in the testing dataset was obtained. And the sensitivity of photosynthesis to the specific variable could be calculated by averaging the sensitivity on all data.

Statistical analysis: Two-way *MANOVA SPSS 11* (*SPSS,* Chicago, IL, USA) with flooding and sampling data was used to test the differences in means for P_N, g_s, E, and WUE responses. The *Tukey* procedure was used to examine pairwise group differences. A Student's *t*-test was used to test for significant means differences between flooded and nonflooded conditions. Differences were considered significant at $p<0.05$.

Results

Photosynthetic characteristics: Long-term soil flooding decreased P_N of *C. cinerascens* by 14.5% ($p<0.05$) (Table 2). Summarizing the results from the P/I and P/C_i curves, soil flooding increased dark respiration by 94.3% in comparison with nonflooded conditions ($p<0.05$). Significant difference was also found in Lc ($p<0.01$) and Ls ($p<0.05$) (Table 3). R_{day} in the flooded condition increased by 79.1% and J_{max} decreased by 32.5% in comparison with the nonflooded condition (Table 4). In our study, no significant variations were found in F_v/F_m, F_v/F_o, q_P, q_N, ETR, and Φ_{PSII} between the two conditions (Table 5). According to the analysis of photosynthetic pigments, long term of soil flooding reduced Chl *a* by 38% ($p<0.05$) and Chl ($a+b$) by 33% ($p<0.05$) (Fig. 1).

Table 2. Daily mean photosynthetic parameters and probability values of *ANOVA* – comparison of the effects of flooding on *C. cinerascens* between 30 and 60 d after soil flooding. Data are mean of six replicates ± SE. % represent the flooded *vs.* nonflooded, [*] $p<0.05$, [**] $p<0.01$, [***] $p<0.001$.

Parameters	Nonflooded	Flooded	[%]	p Condition	Duration	C×D
P_N [µmol m^{-2} s^{-1}]	10.37 ± 0.30	8.87 ± 0.29	85.53	0.010[*]	0.006[**]	0.015[*]
g_s [mol m^{-2} s^{-1}]	0.248 ± 0.007	0.242 ± 0.004	97.58	0.593	0.001[**]	<0.001[***]
E [mmol m^{-2} s^{-1}]	4.66 ± 0.12	4.51 ± 0.11	96.78	0.705	<0.001[***]	<0.001[***]
WUE [mmol mol^{-1}]	2.26 ± 0.05	2.07 ± 0.06	91.59	0.112	0.373	0.742

Table 3. Photosynthetic parameters estimated from the light-response curve. Data are means of three replicates ± SE. % represent the flooded *vs.* nonflooded, different letters represent significant difference at the significant level of 0.05.

Parameter	Condition Nonflooded	Flooded	[%]
R_D [µmol m^{-2} s^{-1}]	1.58 ± 0.09[a]	3.07 ± 0.18[b]	194.3
AQY	0.038 ± 0.001[a]	0.035 ± 0.006[a]	93.6
Lc [µmol m^{-2} s^{-1}]	37.8 ± 2.21[a]	83.7 ± 5.27[b]	221.3
Ls [µmol m^{-2} s^{-1}]	580 ± 18.8[a]	520 ± 36.75[b]	89.6

Artificial neural network model analysis: For both trained dataset and tested dataset, the RBF network showed good performance in predicting the P_N response, which was evidenced by the high correlation (0.999, 0.999) and low absolute errors (0.16, 0.17) between the predicted P_N and the observed values (Table 6). Analysis was carried out on the weightings of neural networks to give a relative importance for each of the network inputs (Fig. 2). As expected, two RBF network models indicated that g_s was the dominant factor in determining of the measured response. The weighting analysis also showed that the effect of VPD > T > C_a > RH > PPFD for the nonflooded model, whereas for the flooded model, the factors were ranked in the order VPD > C_a > RH > PPFD > T. According to the analysis, there were different response traits of P_N between soil flooded ANN model and nonflooded ANN model: higher positive g_s, higher negative E, higher positive T and higher positive T_l than those in flooded condition, this difference also reflected the effect of soil flooding on P_N.

Discussion

Photosynthesis of flooded *C. cinerascens* was 85.5% of that in nonflooded plants throughout the 60 days of flooding. The extent of the reduction of photosynthesis in *C. cinerascens* was similar to some flood-tolerant species (Baruch 1994, Gravatt and Kirby 1998). Flooding is known to affect photosynthesis through changes in stomatal conductance, many wetland species initially close stomata in response to soil flooding (Kozlowski 1984). Numerous studies also pointed out that stomatal closure might be mainly responsible for the decrease in photosynthesis during short-term submergence, but is not the only limiting factor (Bradford 1983). Some factors restricting photosynthetic activity may include decreased Chl content (Macek *et al.* 2006) and Rubisco regeneration capacity (Pezeshki 1994) under flooding stress. In our study, we found that Chl content significantly decreased in *C. cinerascens* during the flooding period. Differences in Chl content in leaves of *C. cinerascens* between two conditions can be assumed as adaptations to different habitat situations. Flooded plants showed lower Chl contents, which agrees with what has also been described from some wetland plants suffering from soil flooding (Chen *et al.* 2005). Significant reduction of J_{max} was observed in our study, which meant that the soil flooding induced the deficiency of Rubisco regeneration rate in *C. cinerascens,* similar response was found in barley plants suffering from soil flooding (Yordanova *et al.* 2003). Under flooding, the reduction in photosynthesis was accompanied by increased dark-respiration rate in leaves (Bragina *et al.* 2004). In this case, a twofold value of the R_D in flooded condition indicated that higher energy expenditure was applied to maintain the

Table 4. Photosynthetic parameters in *C. cinerascens* under nonflooded and flooded conditions. Data are means of three replicates ±SE (n = 3). % represent the flooded *vs*. Nonflooded condition, different letters represent significant difference at the significant level of 0.05.

Parameter	Condition		[%]
	Nonflooded	Flooded	
R_{day} [μmol m^{-2} s^{-1}]	1.34 ± 0.185[a]	2.40 ± 0.351[b]	179.1
V_{cmax} [μmol m^{-2} s^{-1}]	80.0 ± 3.79[a]	77.0 ± 7.21[a]	96.3
J_{max} [μmol m^{-2} s^{-1}]	206.1 ± 16.3[a]	139.3 ± 24.6[b]	67.5
Γ [μmol mol^{-1}]	71.6 ± 1.95[a]	76.2 ± 3.56[a]	106.4
CE	0.105 ± 0.014[a]	0.094 ± 0.007[a]	89.7

Table 5. Chlorophyll fluorescence parameters of *C. cinerascens* under nonflooded and flooded conditions. Data are means of five replicates ± SE. % represent the flooded *vs.* nonflooded, different letters represent significant difference at the significant level of 0.05.

Parameter	Condition		[%]
	Nonflooded	Flooded	
F_v/F_m	0.82 ± 0.00[a]	0.83 ± 0.00[a]	100.7
F_v/F_o	4.61 ± 0.04[a]	4.81 ± 0.09[a]	104.2
q_P	0.72 ± 0.03[a]	0.73 ± 0.03[a]	99.9
q_N	0.267 ± 0.035[a]	0.266 ± 0.031[a]	101.5
ETR [μmol m^{-2} s^{-1}]	27.0 ± 3.36[a]	25.7 ± 2.05[a]	95.4
Φ_{PSII}	0.127 ± 0.016[a]	0.121 ± 0.010[a]	95.4

metabolism in response to soil flooding.

Chl fluorescence has been widely used to reveal the responses of plants to environmental stresses (Maxwell and Johnson 2000, Mauchamp and Méthy 2004). In our study, we did not find any differences in fluorescence parameters between the two experimental conditions. This indicated that there was no damage to photochemical reactions, thus, fluorescence would not provide a good indication of gas exchange of *C. cinerascens.*

Based on the analysis of ANN models, g_s, C_i, E, VPD, T, T_l, C_a, RH, and PPFD contain sufficient information for predicting P_N of *C. cinerascens* in both the nonflooded and flooded conditions. By the low error of P_N predictions the neural networks hold the capacity to model the complex relation among these variables and P_N

of *C. cinerascens.* Analysis of the weightings for biotic and abiotic parameters indicated the strength of influence of each parameter on the development of flooding stress. In both two RFB networks models, g_s had the strongest weighting, the similar results can be found in other studies of influences on soil flooding effects (Mielke *et al.* 2003). Similar response of P_N to E was found in *C. cinerascens,* higher negative E than that in flooded condition suggested that *C. cinerascens* sustained a favourable water status for photosynthesis by the interaction of stomatal closure and low transpiration rates to compensate for a slow water-absorption rate by roots (Pezeshki and Chambers 1985). We can also conclude that nonflooded *C. cinerascens* used as much or more water in transpiration and achieved photosynthetic rates as much as high during photosynthesis occurring under relatively nonlimiting conditions. Abiotic factors also had strong influences on the network. Of these, VPD was found to be the most important for two conditions; this indicated that soil flooding did not alert the P_N/VPD response. Temperature also had a strong influence, possibly causing metabolic processes associated with the flooding stress. Studies showed that shift in the optimum temperature of photosynthesis might be related with changes in the capacity for RuBP regeneration and the ratio of J_{max} and V_{cmax} (Farquhar and von Caemmerer 1982, Yamori *et al.* 2005). In our study, different weightings of T and T_l were found between nonflooded and flooded conditions, which meant that the optimal range of temperature for growth and physiology of

Table 6. The prediction performance of the trained RBF networks. R^2 – correlation coefficient.

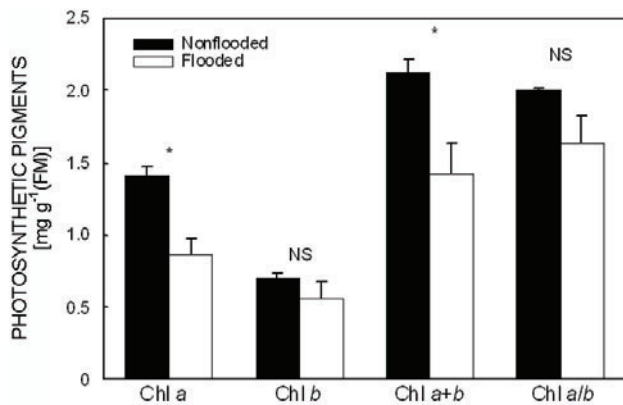| Dataset		R^2	Mean absolute error [μmol(CO$_2$) mol^{-1}]
Nonflooded	Testing subset of the nonflooded dataset	0.999	0.1671
RBF network	Training subset of the nonflooded dataset	0.999	0.1602
Flooded	Testing subset of the flooded dataset	0.999	0.2005
RBF network	Training subset of the flooded dataset	0.999	0.2000

Fig. 1. Chlorophyll (Chl) *a*, Chl *b*, Chl (*a+b*) and the ratio Chl *a*/*b* in leaves of *C. cinerascens* under nonflooded and flooded conditions. *Vertical bars* are SE (*n* = 3), * – significant differences at the level of 0.05, NS – not significant.

Fig. 2. Relative weighting of biotic and abiotic variables in nonflooded and flooded conditions.

C. cinerascens is not likely to be identical to that in the nonflooded condition. The interactions were evidenced by the variation of the J_{max} and the ratio of J_{max} and V_{cmax} between two experimental conditions (Table 4). These clearly illustrate that soil flooding strongly affected the response of P_N to microclimatic variables. Of the studied microclimatic factors, PPFD was the most weakly weighted; the low importance of PFD might be due to the linear relationship between g_s and PPFD, and g_s might be a better measure of P_N. The model possibly uses g_s in preference to PPFD to predict P_N, for another, PPFD was continuously variable across the two conditions, it might not account for so many variations between two conditions in this model.
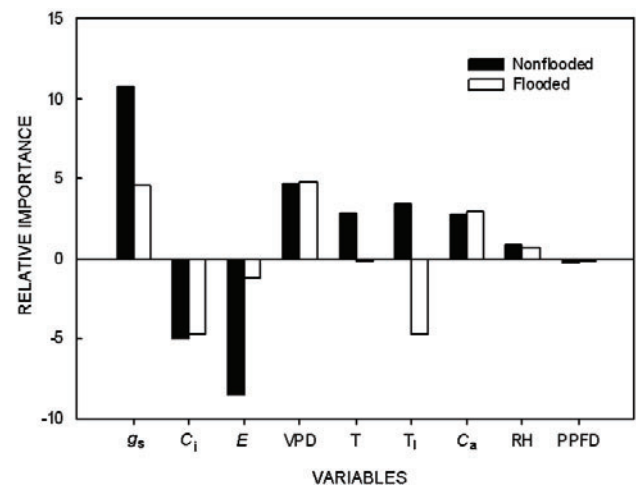
In conclusion, long term of soil flooding resulted in inhibition of photosynthesis of *C. cinerascens*, which was evidenced by the reduced stomatal conductance, the deficiency of regeneration for Rubisco, increase of respiration rate and the diminished Chl content. These data underline the need for better knowledge of quantitative relationships between plant growth characteristics and environmental factors. Among the environmental variables, as revealed by analysis of *MANOVA* and ANN models, stomata closure may be the main factor resulting in the reduction of photosynthesis rate. Furthermore, the different photosynthetic response of *C. cinerascens* found between the nonflooded and flooded conditions would be useful to evaluating of the flood tolerance at the level of individual plant species.

References

Balls, G.R., Palmer-Brown, D., Sanders, G.E.: Investigating microclimatic influences on ozone injury in clover (*Trifolium subterraneum*) using artificial neural networks. – New Phytol. **132**: 271-286, 1996.

Baruch, Z.: Responses to drought and flooding in tropical forage grasses. II. Leaf water potential, photosynthesis rate and alcohol dehydrogenase activity. – Plant Soil **164**: 97-105, 1994.

Bianchini, M., Frasconi, P., Gori, M.: Learning without local minima in radial basis function networks. – IEEE Trans. Neural Networks **6**: 749-756, 1995.

Bradford, K.J.: Effects of soil flooding on leaf gas exchange of tomato plants. – Plant Physiol. **73**: 475-479, 1983.

Bragina, T.V., Ponomareva, Y.V., Drozdova, I.S., Grinieva, G.M.: Photosynthesis and dark respiration in leaves of different ages of partly flooded maize seedlings. – Russ. J. Plant Physiol. **51**: 342-347, 2004.

Brown, C.E., Pezeshki, S.R.: A study on waterlogging as a potential tool to control *Ligustrum sinense* populations in western Tennessee. – Wetlands **20**: 429-437, 2000.

Chen, H.J., Qualls, R.G., Blank, R.R.: Effect of soil flooding on photosynthesis, carbohydrate partitioning and nutrient uptake in the invasive exotic *Lepidium latifolium*. – Aquat. Bot. **82**: 250-268, 2005.

Farquhar, G.D., von Caemmerer, S.: Modeling of photosynthetic responses to environmental conditions. – In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (ed.): Physiological Plant Ecology. II.Water Relation and Carbon Assimilation. Pp. 549-587. Springer-Verlag, Berlin – Heidelberg – New York 1982.

Farquhar, G.D., von Caemmerer, S.V., Berry, J.A.: A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. – Planta **149**: 78-90, 1980.

Genty, B., Briantais, J.M., Baker, N.R.: The relationship between the quantum yield of photosynthetic electron-transport and quenching of chlorophyll fluorescence. – Biochim. Biophys. Acta **990**: 87-92. 1989.

Gravatt, D.A., Kirby, C.J.: Patterns of photosynthesis and starch allocation in seedlings of four bottomland hardwood tree species subjected to flooding. – Tree Physiol. **18**: 411-417, 1998.

Huntingford, C., Cox, P.M.: Use of statistical and neural network techniques to detect how stomatal conductance responds to changes in the local environment. – Ecol. Model. **97**: 217-246, 1997.

Jeong, K.S., Joo, G.J., Kim, H.W., Ha, K., Recknagel, F.:

Prediction and elucidation of phytoplankton dynamics in the Nakdong River (Korea) by means of a recurrent artificial neural network. – Ecol. Model. **146**: 115-129, 2001.

Kozlowski, T.T.: Plant responses to flooding of soil. – Bioscience **34**: 162-167, 1984.

Li, M., Yang, D., Li, W.: Leaf gas exchange characteristics and chlorophyll fluorescence of three wetland plants in response to long-term soil flooding – Photosynthetica **45**: 222-228, 2007.

Liao, C.T., Lin, C.H.: Effect of flooding stress on photosynthetic activities of *Momordica charantia*. – Plant Physiol. Biochem. **32**: 479-485, 1994.

Lichtenthaler, H.K.: Chlorophyll. and carotenoids, pigments of photosynthetic biomembranes. – Methods Enzymol. **148**: 350-382, 1987.

Macek, P., Rejmánková, E., Houdková, K.: The effect of long-term submergence on functional properties of *Eleocharis cellulosa* Torr. – Aquat. Bot. **84**: 251-258, 2006.

Marshall, B., Biscoe, P.V.: A model for C3 leaves describing the dependence of net photosynthesis on irradiance. Derivation. – J. Exp. Bot. **31**: 29-39, 1980.

Mauchamp, A, Méthy, M.: Submergence-induced damage of photosynthetic apparatus in *Phragmites australis*. – Environ. Exp. Bot. **51**: 227-235, 2004.

Maxwell, K., Johnson, G.N.: Chlorophyll fluorescence - a practical guide. – J. Exp. Bot. **51**: 659-668, 2000.

McKevlin, M.R., Hook, D.D., McKee, W.H.: Growth and nutrient use efficiency of water tupelo seedlings in flooded and well drained soil. – Tree Physiol. **15**: 753-758, 1995.

Melesse, A.M., Hanley, R.S.: Artificial neural network application for multi-ecosystem carbon flux simulation – Ecol. Model. **189**: 305-314, 2005.

Mielke, M.S., de Almeida, A.-A.F., Gomes, F.P., Aguilar, M.A.G., Mangabeira, P.A.O.: Leaf gas exchange, chlorophyll fluorescence and growth responses of *Genipa americana* seedlings to soil flooding. – Environ. Exp. Bot. **50**: 221-231, 2003.

Mishra, S.K., Patro, L., Mohapatra, P.K., Biswal, B: Response of senescing rice leaves to flooding stress. – Photosynthetica **46**: 315-317, 2008.

Mommer, L., Pons, T.L., Visser, E.J.W.: Photosynthetic consequences of phenotypic plasticity in response to submergence: *Rumex palustris* as a case study. – J. Exp. Bot. **57**: 283-290, 2006.

Pallas, J.E., Kays, S.J.: Inhibition of photosynthesis by ethylene - a stomatal effect. – Plant Physiol. **70**: 598-601, 1982.

Park, J., Sandberg, I.W.: Universal approximation using radial basis functions network. – Neural Computation **3**: 246-257, 1991.

Pezeshki, S.R.: Responses of baldcypress (*Taxodium distichum*) seedlings to hypoxia: leaf protein content, ribulose-1, 5-bisphosphate carboxylase/oxygenase activity and photosynthesis. Photosynthetica **30**: 59-68, 1994.

Pezeshki, S.R.: Wetland plant responses to soil flooding. – Environ. Exp. Bot. **46**: 299–312, 2001.

Pezeshki, S.R, Chambers, J.L.: Responses of cherrybark oak seedlings to short-term flooding. – Forest Sci. **31**: 760-771, 1985.

Pezeshki, S.R., Pardue, J.H., DeLaune, R.D.: The influence of soil oxygen deficiency on alcohol dehydrogenase activity, root porosity, ethylene production and photosynthesis in *Spartina patens*. – Environ. Exp. Bot. **33**: 565-573, 1993.

Ponnamperuma, F.N.: Effects of flooding on soils. – In: Kozlowski, T.T.(ed.): Flooding and Plant Growth. Pp. 1-44. Academic Press, Orlando – San Diego – San Francisco – New York – London – Toronto – Montreal – Sydney – Tokyo – São Paulo 1984.

Poorter, H.: Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO_2? – Glob. Change Biol. **4**: 693-697, 1998.

Schreiber, U., Bilger, W., Neubauer, C.: Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of *in vivo* photosynthesis. – In: Schulze, E.-D., Caldwell, M.M. (ed.): Ecophysiology of Photosynthesis. Pp. 49-70. Springer-Verlag, Berlin 1994.

Taylor, G.E., Gunderson, C.A.: Physiological site of ethylene effects on carbon dioxide assimilation in *Glycine max*. L. Merr. – Plant Physiol. **86**: 85-92, 1988.

Wasserman, P.D.: Neural Computing: Theory and Practice, Van Nostrand Reinhold, New York 1989.

Yamori, W., Noguchi, K., Terashima, I.: Temperature acclimation of photosynthesis in spinach leaves: analyses of photosynthetic components and temperature dependencies of photosynthetic partial reactions. – Plant Cell Environ. **28**: 536-547, 2005.

Yordanova, R.Y., Alexieva, V.S., Popova, L.P.: Influence of root oxygen deficiency on photosynthesis and antioxidant status in barley plants. – Russ. J. Plant Physiol. **50**: 163-167, 2003.