A meta-analysis of responses of wheat yield formation to elevated ozone concentration

FENG ZhaoZhong^{1,2†}, KOBAYASHI Kazuhiko², WANG XiaoKe¹ & FENG ZongWei¹

¹ State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085;

² Department of Global Agricultural Sciences, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo 113-8657, Japan

The meta-analysis method was applied to quantitatively investigate effects of the elevated ozone concentration ([O₃]) on chlorophyll concentration, gas exchange and yield components of wheat. There were 39 effective references through Web of Science (ISI, USA) and Chinese journal full-text database (CNKI, China). The results of meta-analysis indicated that elevated [O₃] decreased grain yield, grain weight, grain number per ear, ear number per plant and harvest index by 26%, 18%, 11%, 5% and 11%, respectively, relative to ambient air. The decrease in leaf physiological characters was much greater than that in yield when wheat was exposed to elevated [O₃], while light-saturated photosynthetic rate (Asat), stomatal conductance (Gs) and chlorophyll content (Chl) decreased by 40%, 31%, and 46%, respectively. The responses to elevated [O₃] between spring wheat and winter wheat were similar. Most of the variables showed a linear decrease trend with an increase of [O₃]. The most significant decrease for Asat, Gs and Chl was found in grain filling stage. Elevated [CO₂] could significantly ameliorate or offset the detrimental effects caused by elevated [O₃].

meta-analysis, elevated [CO₂], wheat, ozone, gas exchange, yield

Surface ozone (O₃) was the most important phytotoxic gaseous pollutant to the terrestrial vegetation in many parts of the world^[1]. Since 1960s, elevated ambient O₃ concentration ([O₃]) in industrialized countries was reported to reduce growth and yield of C3 crops^[2,3]. In the past decades, tropospheric [O₃] increased rapidly as a result of overuse of fossil fuel and nitrogen fertilizer^[4]. Nearly one-quarter of the earth's surface is currently at risk from elevated [O₃] in excess of 60 ppb (1 ppb = 2 × 10⁻⁹ g/L) during mid-summer, and [O₃] increased at a rate of 0.3%–2.0% annually^[5]. Models predicted that tropospheric [O₃] could rise 20%–25% by 2050, and further increase 40%–60% by 2100 if the current emission trends continue^[4]. In addition, due to long distance transport of NO_x and VOCs, [O₃] higher than the critical level to plants appeared frequently in agricultural, forest and remote rural areas^[6]. Surface O₃ has been currently

assumed as one of the major environmental issues in some rural and urban regions^[7,8].

Entering into mesophyll through leaf stomata, O₃ can directly react with the plasmalemma through ozonolysis, or it can be converted into reactive oxygen species, including hydrogen peroxide that alter cellular components and can lead to cell death and accelerated senescence^[9]. At the whole plant level, chronic O₃ exposure can lead to visible leaf injuries, e.g. chlorosis, brown lesions and necrosis in wheat, chlorosis, brown lesions and furring in rice^[10]. Elevated [O₃] could also induce reductions in biomass and yield of most plants, although

Received July 1, 2008; accepted October 23, 2008

doi: 10.1007/s11434-008-0552-6

†Corresponding author (email: zhzhfeng201@163.com)

Supported by National Natural Science Foundation of China (Grant No. 30670387), Eco-Frontier Fellowship of the Ministry of Environment, Japan (Grant No. 07-C062-03) and Ministry of Science and Technology of People's Republic China with 973 Project (Grant No. 2002CB410803)

the observed responses varied with species and exposure conditions^[3,7,11–13]. Wheat was one of the most sensitive species to O₃^[14,15]. Lower ambient [O₃] reduced the yield by 40% in winter wheat relative to carbon-filtered air^[16]. However, there existed a large difference in the detrimental effects of O₃. The variability was not only resulted from exposure dose (concentration × time) and genetic differences, but also O₃ exposure duration and fumigation regimes. Pleijel et al.^[17] investigated field-grown spring wheat exposed to the same ozone dose, before anthesis or after onset of anthesis, and concluded that ozone exposure between anthesis and the end of grain filling is much more effective in decreasing the wheat grain yield than ozone exposure occurred before anthesis. Meyer et al.^[18] found that dynamic [O₃] fumigation regime ([O₃] peak) induced larger yield loss than constant [O₃] exposure regime did under equal dose-conditions.

To assess the effects of elevated [O₃] on growth and yield, it is indispensable to cover the interaction between rising [O₃] with other environmental factors, such as elevated [CO₂], drought and high temperature. Factors that influence stomatal conductance (Gs) can alter the flux of O₃ into intercellular spaces of the leaf. Water stress or elevated [CO₂] is accompanied by decreased Gs, which in turn less ozone reaches the inner leaf tissues, thereby decreasing ozone injury to the leaves. On the other hand, higher humidity or soil water content aggravated the detrimental effects of O₃ due to increased stomatal opening^[19,20]. It can be expected that large variability could occur between individual studies due to the complexity of factors. Therefore, it is necessary to combine various factors to reveal quantitatively the detrimental effects of elevated [O₃] on growth of crops and study what the mechanisms are.

Meta-analysis is a quantitative approach that estimates a mean relative response from individual studies to find general trend and differences. It developed rapidly since it was successfully introduced into the field of ecology and evolutionary biology at 1990s^[21–23]. In 1999, meta-analysis application in ecology was published in a special issue of *Ecology*, which systematically discussed case studies, development and problems on its use in ecology^[22]. With the increasing concerns on global change issues, meta-analysis has been adopted in this field extensively, e.g. the responses of ecosystem to global warming, rising [CO₂] and elevated [O₃], the effects of land use and

management on climate change^[21–23]. Lei et al.^[21] described the principles, steps, advantages and disadvantages of meta-analysis and reviewed its application in the field of climate change. However, very few studies used the meta-analytic technique in the field of ecology in China^[24,25].

In this review, we integrated all the relevant individual studies and used meta-analytic procedures to quantitatively determine the mean effects of elevated [O₃] on photosynthesis and yield loss of wheat, relative to ambient [O₃]. In addition, the sources of variations, such as wheat genotypes, fumigation duration, developmental stages and elevated [CO₂] were also discussed. The results will be crucial to forecast future food safety induced by global atmospheric and environmental changes.

1 Materials and methods

1.1 Development of database

A database of effects of O₃ on wheat growth and yield loss was compiled by surveying the peer-reviewed literature with the Web of Science (ISI, USA) and Chinese Journal Full-Text Database (CNKI, China). Keyword searches were made for O₃ and wheat, covering the period 1980 through 2007. To be included in this meta-analysis, articles and measurements have to meet the following criteria: (i) ambient and elevated [O₃] treatments were included in each study; (ii) ozone fumigation was more than ten days; (iii) only one paper was selected if the data were reported in another one; (iv) responses have been measured with respect to yield (Y) and its components, such as individual grain weight (GW), grains per ear (GNE) and ears per plant (ENP), harvest index (HI), above-ground biomass (Bs), light-saturated photosynthetic rate (Asat), stomatal conductance (Gs) and chlorophyll content (Chl). Based on these criteria, 39 articles were used for this meta-analysis. Meta-analytic methods require that individual observations be statistically independent. Parameter values were considered independent if they were made on different cultivars, [O₃], different dates of measurements and additional treatments in the same experiment, following previous meta-analyses^[26]. The mean value (X_C and X_E), the standard deviations and the replication in ambient [O₃] (as control) and elevated [O₃] (as treatment) were recorded in a database, together with the categorical

information. Data were recorded directly from tables and texts and digitized from figures using data extraction software (GRAFULA, Russia). To explain variations in the response of wheat to elevated $[O_3]$, 5 categories were included as follows: (i) mean $[O_3]$ (30–59, 60–89, 90–119 and ≥ 120 ppb); (ii) wheat types (spring wheat versus winter wheat); (iii) developmental stages (seedling, booting-anthesis and grain filling); (iv) durations of leaf fumigation (3–10, 11–20 and >20 d); (v) additional treatments (no additional treatments, combination of elevated $[O_3]$ and elevated $[CO_2]$).

1.2 Meta analysis

To estimate the treatment effects, the natural log of the response ratio (r) was used as the metric for analysis, where r is the ratio of variables in elevated $[O_3]$ (X_E) divided by variables in ambient $[O_3]$ (X_C)^[19,26]. Mean response ratio was carried out following the techniques in Curtis and Wang^[26], using MetaWin 2.0 statistical software. The mixed-model approach (random effect) was used based on the assumption of random variation in responses among studies. The approach used here was similar to that of reported previously in a single species^[19,27]. Many studies did not report standard deviations or standard errors with replicate size, which would allow computation of sample variance. In this case, re-sampling was used to develop a variance of the effect size^[28]. An unweighted meta-analysis was performed with significance determined from 95% confidence intervals (CI), which were calculated using bootstrap methods^[28].

Relative to ambient $[O_3]$, the percentage change of the variables at elevated $[O_3]$ was expressed as $(r-1) \times 100\%$ ^[27]. $r = 1$ indicated that plant responses are the same in CF and elevated $[O_3]$ treatments, and therefore no percentage change (0%). Negative percentage change ($r < 1$) indicates a decrease in the plant variable in response to elevated $[O_3]$ and positive values indicate an increase. Response to O_3 treatment is assumed to be significant if the 95% CI did not overlap zero and the difference between categorical variables was considered significant if the 95% CIs did not overlap^[19,26].

2 Results and analysis

2.1 Overall effects of elevated $[O_3]$ on photosynthesis and yield component in wheat

From Figure 1, elevated $[O_3]$ induced much larger det-

rimental effects on physiological characteristics than that on yield. Relative to ambient $[O_3]$, more than 30% decreases in physiological characteristics including Asat, Gs and Chl were found, when wheat was exposed to elevated $[O_3]$. The largest decrease (46%) was in Chl with the 95% CI of 39%–53%. Elevated $[O_3]$ decreased Asat by 40%, which might be from a combination of decreases of Chl and Gs (31%). Across all studies, mean $[O_3]$ of 77 ppb decreased grain yield by 26%, relative to the average ambient $[O_3]$ of 35 ppb. The yield loss mainly resulted from a combination of lower GW (–18%), GNE (–11%) and ENP (–5%). HI was also reduced by more than 11%, although Bs did not show significant differences between elevated and ambient $[O_3]$ treatments.

Figure 1 Effects of elevated $[O_3]$ on wheat growth and yield components. Symbols represent the mean percent change at elevated $[O_3]$ relative to ambient air and the bars show the 95% confidence intervals (CIs). The degrees of freedom are given in parentheses following bars. Average ambient and elevated $[O_3]$ are given on the y-axis, respectively. Abbreviations for parameters are described as follows. Chl, chlorophyll content; Gs, stomatal conductance; Asat, light-saturated photosynthetic rate; GW, individual grain weight; ENP, ears per plant; GNE, grains per ear; Bs, above-ground biomass; HI, harvest index; Y, yield.

2.2 Factors analysis

(i) The effect of wheat types. All investigated variables showed no significant difference between winter wheat and spring wheat in the responses to elevated $[O_3]$ (Figure 2), suggesting similar responses to elevated $[O_3]$ despite different ecological types.

(ii) The effects of developmental stages and leaf ozone exposure duration. Here, we compare the responses of physiological character of leaves to elevated

Figure 2 Effects of elevated [O₃] on spring wheat and winter wheat. Symbols represent the mean percent change at elevated [O₃] relative to ambient air and the bars show the 95% confidence intervals (CIs). The degrees of freedom are given in parentheses following bars. Average ambient and elevated [O₃] are given on the y-axis, respectively. Abbreviations for parameters are described as follows. Chl, chlorophyll content; Gs, stomatal conductance; Asat, light-saturated photosynthetic rate; GW, individual grain weight; ENP, ears per plant; GNE, grains per ear; HI, harvest index; Y, yield.

[O₃] at different development stages (Figure 3). The detrimental impacts of O₃ increased with developmental stages from young to old. From the mean effects, the data of Asat, Gs and Chl showed the least decrease during the vegetative growing stage and the largest during grain filling stage. In comparison with ambient [O₃], elevated [O₃] did not cause significant decreases in Asat, Gs and Chl at the vegetative stage, but the decreases at grain filling stage were significant larger than those at other stages.

There was a progressive decrease with increasing duration of leaf exposure to elevated [O₃] in Asat and Gs (Figure 4). Asat and Gs were decreased by 15% and 4% within 10 d of O₃ exposure, respectively. But the decreases were 71% and 58%, respectively, when O₃ exposure duration was more than 20 d.

(iii) The effect of [O₃]. Except for ENP and Chl, the detrimental effect of O₃ on leaf photosynthesis and Bs was linearly greater as the average daily [O₃] increased (Figure 5). Compared with ambient [O₃], the yield loss was 17% and 24% induced by averaged [O₃] of 51 ppb and 75 ppb, respectively. Similar trend was also found in GW. Asat appeared to be very sensitive to elevated [O₃].

Figure 3 Response of wheat to elevated [O₃] at different developmental stages. Symbols represent the mean percent change at elevated [O₃] relative to ambient air and the bars show the 95% confidence intervals (CIs). The degrees of freedom are given in parentheses following bars. Average ambient and elevated [O₃] are given on the y-axis, respectively. Abbreviations for parameters are described as follows. Chl, chlorophyll content; Gs, stomatal conductance; Asat, light-saturated photosynthetic rate.

Figure 4 Response of wheat leaf to elevated [O₃] at different exposure duration. Symbols represent the mean percent change at elevated [O₃] relative to ambient air and the bars show the 95% confidence intervals (CIs). The degrees of freedom are given in parentheses following bars. Average ambient and elevated [O₃] are given on the y-axis, respectively. Abbreviations for parameters are described as follows. Gs, stomatal conductance; Asat, light-saturated photosynthetic rate.

It was decreased by 33% at a mean of 49 ppb of [O₃] and by more than 50% at 81 ppb, respectively. Moreover, lower than 60 ppb of [O₃] significantly reduced all investigated variables with an exception of ENP and Gs (Figure 5).

(iv) The effect of elevated [CO₂]. Based on the average effect, elevated [CO₂] significantly ameliorated or moderated the deleterious effects of O₃ on photosynthesis and yield (Figure 6). There was no significant de-

Figure 5 Effects of different concentrations of elevated $[O_3]$ on wheat growth and yield components. Symbols represent the mean percent change at elevated $[O_3]$ relative to ambient air and the bars show the 95% confidence intervals (CIs). The degrees of freedom are given in parentheses following bars. Average ambient and elevated $[O_3]$ are given on the y-axis, respectively. Abbreviations for parameters are described as follows. Chl, chlorophyll content; Gs, stomatal conductance; Asat, light-saturated photosynthetic rate; GW, individual grain weight; ENP, ears per plant; GNE, grains per ear; Bs, above-ground biomass; HI, harvest index; Y, yield.

Figure 6 The interactive effect of elevated $[O_3]$ on wheat with no additional treatments and with elevated $[CO_2]$ (>500 ppm). Symbols represent the mean percent change at elevated $[O_3]$ relative to ambient air and the bars show the 95% confidence intervals (CIs). The degrees of freedom are given in parentheses following bars. Average ambient and elevated $[O_3]$ are given on the y-axis, respectively. Abbreviations for parameters are described as follows. Chl, chlorophyll content; Gs, stomatal conductance; Asat, light-saturated photosynthetic rate; GW, individual grain weight; ENP, ears per plant; GNE, grains per ear; Bs, above-ground biomass; HI, harvest index; Y, yield.

crease in grain yield, HI or GNE under combined elevation of $[CO_2]$ and $[O_3]$ (overlap with 0). For those studies with no additional treatments, elevated $[O_3]$ decreased yield, GW and ENP by 30%, 22% and 11%, respectively. However, the decreases were only 2%, 3% and 5% at elevated $[CO_2]$, respectively, relative to ambient $[CO_2]$. Besides, the reduction in Asat under a combination of elevated $[O_3]$ and $[CO_2]$ was 35% of that under ambient $[CO_2]$ and elevated $[O_3]$ (Figure 6). Similar trend was also found in Gs. Compared with the average (-31%) across all studies (Figure 1), elevated $[O_3]$ decreased Gs by 45% at ambient $[CO_2]$, and no other additional treatments, but only by 9% at elevated $[CO_2]$.

3 Discussion

With meta-analysis, we assessed quantitatively the effects of elevated $[O_3]$ on physiological characters and grain yield of wheat. Results indicated that the average $[O_3]$ of 77 ppb decreased grain yield by 26%, relative to current ambient $[O_3]$, with a 95% CI of 20%–32% in spite of variations in the response observed among studies. It can be inferred that wheat production in the near future may suffer serious losses if ambient $[O_3]$ keeps rising. From our meta-analysis, the most important yield component responsible for grain yield reduction was the decrease of GW (18%), although both ENP and GNE showed significant decreases at elevated $[O_3]$. It is suggested that grain filling was damaged most by elevated $[O_3]$ among the growth processes. Feng et al.^[29] found elevated $[O_3]$ significantly increased the number of empty grains in wheat with open-top chambers.

Like photosynthetic rate and photosynthetic pigment, the physiological variables of leaves were much more sensitive to $[O_3]$ than yield. Within 135 measurements, averaged $[O_3]$ of 79 ppb decreased Chl by 46%, suggesting that elevated $[O_3]$ significantly accelerated leaf senescence. Early senescence of leaf by O_3 was also found in other crops such as soybean^[30], potato^[31] and corn^[32]. The significant decrease in Asat directly affected the fixation of carbohydrate and transformation to grain. The decrease in Gs indicated that less O_3 entered into mesophyll cells, while the absorption of atmospheric CO_2 for leaves was also decreased at the same time.

Our meta-analysis showed winter wheat and spring wheat had similar response to O_3 in all investigated variables (Figure 2). From Figure 2, mean exposed $[O_3]$

during winter wheat growth was reported markedly higher than that of spring wheat, which was caused by the difference in $[O_3]$ calculation modes. Spring wheat was mostly studied in Europe, in which reported $[O_3]$ was the average during whole developmental stages regardless of fumigation or not. However, winter wheat was usually fumigated after jointing stage, and $[O_3]$ was calculated based on actual fumigation days, namely excluding days of no O_3 fumigation.

From the analysis of published data on Asat, Gs and Chl, we found the most decrease occurred in grain filling stage across all developmental stages, in agreement with the results of a meta-analysis on soybean^[19]. Pleijel et al.^[17] exposed field-grown spring wheat to the same O_3 dose at different stages, and reported that O_3 exposure at grain filling stage induced larger yield loss than that before anthesis. However, it can't be concluded that grain filling stage is the most sensitive to O_3 . In general, chronic O_3 induced negative effects on plant physiological characters only if O_3 flux in mesophyll reaches a much high level through accumulation effect, and further affects biomass and yield. This was confirmed by the results of Figure 4. Relative to ambient $[O_3]$, Asat and Gs showed a significant decrease, only when wheat was exposed to elevated $[O_3]$ of about 80 ppb for more than 10 days, although the decreasing trends appeared within 10 days of fumigation (Figure 4).

It is well documented that elevated $[CO_2]$ significantly decreased Gs^[29,33], which would decrease the O_3 flux into intercellular spaces of the leaf. Consequently, it may be expected that the detrimental effects of O_3 on plants would be less under stress conditions than under

non-stress conditions. This notion was supported by our analysis. From Asat and Chl, the decreases induced by elevated $[O_3]$ were less at elevated $[CO_2]$ than those at ambient $[CO_2]$. Elevated $[CO_2]$ also significantly ameliorated the large decrease in Gs induced by elevated $[O_3]$ (Figure 6), implying that O_3 flux into leaves was reduced significantly. Our result was consistent with Wittig et al.^[20] who investigated the effects of elevated $[CO_2]$ on the response of Gs of trees to elevated $[O_3]$. However, Morgan et al.^[19] indicated that elevated $[CO_2]$ significantly increased the reduction in Gs induced by elevated $[O_3]$, relative to ambient $[CO_2]$. At the individual level, grain yield losses were partially or completely ameliorated by elevated $[CO_2]$ in wheat. It was attributed to the improvement in synthesis of carbohydrates and transportation to grains and thus an increase in GW and ENP when wheat was planted at elevated $[CO_2]$ ^[34]. Similar results were also found in the meta-analysis of soybean^[19].

In summary, this study quantitatively investigated the effects of elevated $[O_3]$ on yield formation and photosynthetic physiology by using a meta-analytic technique. Our meta-analysis indicated that the decrease in GW was the main cause of yield loss (26%) induced by a mean $[O_3]$ of 77 ppb. The response of physiological characters to O_3 was more sensitive than that of yield. Elevated $[CO_2]$ significantly alleviated the negative effects of elevated $[O_3]$ on wheat. This study is a case of meta-analysis applied in the field of atmospheric environmental change. We hope domestic researchers could apply meta-analytic technique into ecological research, especially in the field of global climate change.

- 1 Krupa S, McGrath M T, Andersen C P, et al. Ambient ozone and plant health. *Plant Dis*, 2001, 85: 4—12
- 2 Brasher E P, Fieldhouse D J, Sasser M. Ozone injury in potato variety trials. *Plant Dis Rep*, 1973, 57: 542—544
- 3 Heagle A S. Ozone and crop yield. *Ann Rev Phytopathol*, 1989, 27: 397—423
- 4 Meehl G A, Stocker T F, Collins W D, et al. *Global Climate Projections*. Cambridge: Cambridge University Press, 2007
- 5 Fowler D, Cape J N, Coyle M, et al. Modelling photochemical oxidant formation, transport, deposition and exposure of terrestrial ecosystems. *Environ Pollut*, 1999, 100: 43—55
- 6 Ashmore M R. Assessing the future global impacts of ozone on vegetation. *Plant Cell Environ*, 2005, 28: 949—964
- 7 Karnosky D, Skelly J, Percy K, et al. Prospectives regarding 50 years of research on effects of tropospheric ozone air pollution on US forests. *Environ Pollut*, 2007, 147: 489—506
- 8 Prather M, Gauss M, Berntsen T, et al. Fresh air in the 21st century? *Geophys Res Lett*, 2003, 30(2): 1100
- 9 Long S P, Naidu S L. Effects of oxidants at the biochemical, cell and physiological levels. In: Treshow M, ed. *Air Pollution and Plants*. London: John Wiley, 2002. 69—88
- 10 Bai Y M, Guo J P, Wang C Y, et al. The reaction and sensitivity experiment of O_3 on rice and winter wheat (in Chinese). *Chin J Eco-Agr*, 2002, 10(1): 13—16
- 11 Benton J, Fuhrer J, Gimeno B S, et al. An international cooperative programme indicates the widespread occurrence of ozone injury on crops. *Agr Ecosyst Environ*, 2000, 78: 19—30
- 12 Feng Z W, Jin M H, Zhang F Z, et al. Effects of ground-level ozone (O_3) pollution on the yields of rice and winter wheat in the Yangtze River Delta. *J Environ Sci*, 2003, 15: 360—362

- 13 Fuhrer J, Booker F. Ecological issues related to ozone: agricultural issues. *Environ Int*, 2003, 29: 141—154
- 14 Mills G, Buse A, Gimeno B, et al. A synthesis of AOT40-based response functions and critical levels of ozone for agricultural and horticultural crops. *Atmos Environ*, 2007, 41: 2630—2643
- 15 Wang X K, Zheng Q W, Yao F F, et al. Assessing the impact of ambient ozone on growth and yield of a rice (*Oryza sativa* L.) and a wheat (*Triticum aestivum* L.) cultivar grown in the Yangtze Delta, China, using three rates of application of ethylenediurea (EDU). *Environ Pollut*, 2007, 148: 390—395
- 16 Wahid A, Maggs R, Shamsi S R A, et al. Air pollution and its impacts on wheat yield in the Pasistan Punjab. *Environ Pollut*, 1995, 88: 147—154
- 17 Pleijel H, Danielsson H, Gelang J, et al. Growth stage dependence of the grain yield response to ozone in spring wheat (*Triticum aestivum* L.). *Agr Ecosyst Environ*, 1998, 70: 61—68
- 18 Meyer U, Kollner B, Willenbrink J, et al. Physiological changes on agricultural crops induced by different ambient ozone exposure regimes. I. Effects on photosynthesis and assimilate allocation in spring wheat. *New Phytol*, 1997, 136: 645—652
- 19 Morgan P B, Ainsworth E A, Long S P. How does elevated ozone impact soybean? A meta-analysis of photosynthesis, growth and yield. *Plant Cell Environ*, 2003, 26: 1317—1328
- 20 Wittig V E, Ainsworth E A, Long S P. To what extent do current and projected increases in surface ozone affect photosynthesis and stomatal conductance of trees? A meta-analytic review of the last 3 decades of experiments. *Plant Cell Environ*, 2007, 30: 1150—1162
- 21 Lei X D, Peng C H, Tian D L, et al. Meta-analysis and its application in global change research. *Chin Sci Bull*, 2006, 52(3): 289—302
- 22 Osenberg C W, Sarnelle O, Cooper S, et al. Resolving ecological questions through meta-analysis: Goals, metrics and models. *Ecology*, 1999, 80: 1105—1117
- 23 Peng S L, Tang X Y. Meta-analysis and its application in ecology (in Chinese). *J Ecol*, 1998, 17(5): 74—79
- 24 Zheng F Y, Peng S L. Meta-analysis of prey relationships (in Chinese). *Acta Ecol Sin*, 1999, 19 (4): 448—452
- 25 Zheng F Y, Peng S L. Meta-analysis of the response of plant eco-physiological variables to doubled atmospheric C concentrations (in Chinese). *Acta Botan Sin*, 2001, 43 (11): 1101—1109
- 26 Curtis P S, Wang X. A meta-analysis of elevated CO₂ effects on woody plant mass, form and physiology. *Oecologia*, 1998, 113: 299—313
- 27 Ainsworth E A, Davey P A, Bernacchi C J, et al. A meta-analysis of elevated [CO₂] effects on soybean (*Glycine max*) physiology, growth and yield. *Global Change Biol*, 2002, 8: 695—709
- 28 Adams D C, Gurevitch J, Rosenberg M S. Resampling tests for meta-analysis of ecological data. *Ecology*, 1997, 78: 1277—1283
- 29 Feng Z Z, Yao F F, Chen Z, et al. Response of gas exchange and yield components of field-grown *Triticum aestivum* L. to elevated ozone in China. *Photosynthetica*, 2007, 45: 441—446
- 30 Dermody O, Long S P, DeLucia E H. How does elevated CO₂ or ozone affect the leaf-area index of soybean when applied independently? *New Phytol*, 2006, 169: 145—155
- 31 Donnelly A, Craigon J, Black C R, et al. Does elevated CO₂ ameliorate the impact of O₃ on chlorophyll content and photosynthesis in potato (*Solanum tuberosum*)? *Physiol Plant*, 2001, 111: 501—511
- 32 Leitao L, Bethenod O, Biolley J P. The impact of ozone on juvenile maize (*Zea mays* L.) plant photosynthesis: Effects on vegetative biomass, pigmentation, and carboxylases (PEPc and Rubisco). *Plant Biol*, 2007, 9: 478—488
- 33 Ainsworth E A, Rogers A. The response of photosynthesis and stomatal conductance to rising [CO₂]: mechanisms and environmental interactions. *Plant Cell Environ*, 2007, 30: 258—270
- 34 Wall G W, Garcia R L, Kimball B A, et al. Interactive effects of elevated carbon dioxide and drought on wheat. *Agron J*, 2006, 98: 354—381