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Climatic warming changes plant photosynthesis and its temperature dependence in a temperate steppe of northern China

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Abstract

Warming responses of photosynthesis and its temperature dependence in two C_3 grass (*Agropyron cristatum*, *Stipa krylovii*), one C_4 grass (*Pennisetum centrasiaticum*), and two C_3 forb (*Artemisia capillaris*, *Potentilla acaulis*) species in a temperate steppe of northern China were investigated in a field experiment. Experimental warming with infrared heater significantly increased daily mean assimilation rate (A) in *P. centrasiaticum* and *A. capillaris* by 30 and 43%, respectively, but had no effects on other three species. Seasonal mean A was 13, 15, and 19% higher in the warmed than control plants for *P. centrasiaticum, A. capillaries*, and *S. krylovii*, respectively. The mean assimilation rate in *A. cristatum* and *P. acaulis* was not impacted by experimental warming. All the five species showed photosynthetic acclimation to temperature. The optimum temperature for photosynthesis (T_{opt}) and the assimilation rate at T_{opt} in the five species increased by 0.33–0.78 °C and 4–27%, respectively, under experimental warming. Elevated temperature tended to increase the maximum rate of ribulose-1,5-bisphosphate (RuBP) carboxylation (V_{cmax}) and the RuBP regeneration capacity (J_{max}) in the C_3 plants and carboxylation efficiency and the CO_2-saturated photosynthetic rate in the C_4 plant at higher leaf temperature, as well as the optimum temperatures for the four parameters. Our results indicated that photosynthetic responses to warming were species-specific and that most of the species in the temperate steppe of northern China could acclimate to a warmer environment. The changes in the temperature dependence of V_{cmax} and J_{max}, as well as the balance of these two processes altered the temperature dependence of photosynthesis under climatic warming.

Keywords: Warming; C_3 plants; C_4 plants; Photosynthesis; Temperature dependence

1. Introduction

Photosynthesis is the fundamental basis for carbon (C) accumulation, growth, and biomass production of plants. Photosynthetic responses to rising global mean temperature of terrestrial plants can potentially alter ecosystem C balance and cycling (Gunderson et al., 2000; Rustad et al., 2001). Previous studies have shown that climatic warming may directly stimulate (Chapin and Shaver, 1996; Apple et al., 2000), restrain indirectly through warming-induced water stress (Callaway et al., 1994; Roden and Ball, 1996; Pearson and Dawson, 2003), or do not impact photosynthesis of plant species (Nijs et al., 1996; Loik et al., 2000; Starr et al., 2000; Llorens et al., 2003, 2004). The inconsistent observations suggest plant photosynthesis in response to climatic warming might be species specific. Differential responses of photosynthesis to rising temperature could change C accumulation, growth, and biomass production of different plant species, which in turn affects their competitive abilities, coverage, and dominance in the community. Therefore, a better understanding of the responses of photosynthesis in different plant species and/or functional types to increased temperature could help predict the potential changes in species composition and ecosystem C cycling under global warming.

Long-term exposure to changes in temperature can result in plant acclimation. Thermal acclimation of photosynthesis refers to the shift in the photosynthesis-temperature relationship of plants under the altered temperature regime (Billings et al., 1971; Berry and Björkman, 1980). By changing the optimum temperature of photosynthesis, plants can keep efficient photosynthesis at the new growth temperature (Berry and Björkman, 1980). Most studies on thermal acclimation of photosynthesis were

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conducted in the laboratory with constant temperature regimes (Gunderson et al., 2000; Xiong et al., 2000; Bolstad et al., 2003; Yamori et al., 2005). However, there are strong seasonal and diurnal variability in the magnitudes of temperature increase under global warming (IPCC, 2007). Therefore, consistent changes in temperature used in the laboratory are obviously unable to simulate the realistic temperature changes under natural conditions (Loik et al., 2000; Llorens et al., 2004).

Various hypotheses have been proposed to clarify the mechanisms of temperature acclimation in photosynthesis (Hikosaka et al., 1999). According to the models of Farquhar et al. (1980) and Farquhar and Von Caemmerer (1982), the balance between carboxylation (V_{cmax}) and regeneration (J_{max}) of ribulose-1,5-bisphosphate (RuBP) determines the temperature dependence of photosynthesis. Experimental evidences have shown that seasonal temperature variations can alter the balance between V_{cmax} and J_{max} (Hikosaka et al., 1999; Bunce, 2000; Wilson et al., 2000; Onoda et al., 2005a,b; Borjigidai et al., 2006). Therefore, we hypothesize that warming will shift the balance between V_{cmax} and J_{max}, which will potentially contribute to the changes in temperature dependence of photosynthesis under climatic warming.

The temperate steppe in northern China represents the regional vegetation in the vast arid and semiarid area across the Eurasian continent and is predicted to be sensitive to climate change (Christensen et al., 2004). This study was conducted to examine warming effect on the photosynthesis and its temperature dependence in the co-existing C_3 and C_4 plants in the temperate steppe of northern China. Two C_3 grass (*Agropyron cristatum*, *Stipa krylovii*), two C_3 forb (*Artemisia capillaris*, *Potentilla acaulis*), and one C_4 grass species (*Pennisetum centrasiaticum*) that co-occur in a temperate steppe of northern China were planted under the ambient and elevated temperatures manipulated with an infrared heater in the field. Our specific objectives are to address the following questions: (1) how does climatic warming affect photosynthesis of different plant species in the temperate steppe of northern China? (2) does photosynthesis of different species acclimate to climatic warming and to what extent? (3) what biochemical mechanisms are involved in the changes in temperature dependence of photosynthesis? Given the intrinsic differences in ecophysiology among species, we hypothesize that effects of climatic warming on plant photosynthesis and its temperature dependence are dependent on species identity.

2. Materials and methods

2.1. Study site

The study was carried out in Duolun County (42°2′N, 116°17′E), a semiarid area located in Inner Mongolia, China. Mean annual precipitation in this area is 385.5 mm, with peaks in July and August. Mean monthly air temperatures ranges from 18.9 °C in July and −17.5 °C in January, with an annual mean temperature of 2.1 °C. The soil could be classified as chestnut soils (Chinese classification) or Calcic-orthic Aridisol in the US Soil Taxonomy classification, with 62.75 ± 0.04% sand, 20.3 ± 0.01% silt, and 16.95 ± 0.01% clay. Mean bulk density is 1.31 g cm^{-3} and pH value is 6.84 ± 0.07. The predominant species are *Stipa krylovii*, *Agropyron cristatum*, *Artemisia capillaris*, *Potentilla acaulis*, and *Cleistogenes squarrosa*, which grow in mixture with the mean density of 200–300 individuals/m^2.

2.2. Experimental design

Two 3 m × 4 m plots were dug to a depth of 0.45 m. One plot was heated continuously using the infrared heater and the other was the control. One 1.65 m × 0.15 m infrared heater (Kalglo Electronics Inc, Bethlehem, Pennsylvania) was suspended 2.25 m above the ground in the warmed plot. Soil temperatures were spatially uniform in the warmed plots in this study and were also reported in a previous study (Wan et al., 2002). In the control plot, one "dummy" heater with the same shape and size as the infrared heater was suspended 2.25 m high to simulate the shading effects of the heater. The distance between the control and the warmed plot was approximately 5 m to avoid heating the control plot by the infrared heater. Soil temperature was measured by a Longstem Thermometer 6310 (Spectrum Technologies Inc., Plainfield, USA) and soil volumetric water moisture was measured by a Diviner 2000 Portable Soil Moisture Probe (Sentek Pty Ltd., Balmain, Australia).

2.3. Plant materials

Two C_3 grass (*Stipa krylovii*, *Agropyron cristatum*), two C_3 forb (*Artemisia capillaris*, *Potentilla acaulis*) and one C_4 grass species (*Pennisetum centrasiaticum*) that co-occur in a temperate steppe of northern China were selected. Seedlings with similar size were transplanted from a nearby field to PVC tubes in the middle May 2005. PVC tubes (11 cm in internal diameter and 50 cm in depth) were placed in the two 3 m × 4 m plots, buried to the depth of 45 cm belowground, and filled with sieved and fully mixed chestnut soil. Two individuals of one species were planted per tube. Twenty tubes were replicated for one species in each plot. All the tubes were placed randomly in both the control and warmed plots. Two weeks after transplanting, the warmed plot was continuously heated (24 h day^{-1}) with an infrared heater till the end of the growing season (late September).

2.4. Photosynthesis and chlorophyll fluorescence measurements

An open gas-exchange system (Li-6400; Li-Cor, Inc., Lincoln, NE, USA) with a 6-cm^2 clamp-on leaf cuvette was used to measure gas exchange. Three tubes per species in each of the treatments were randomly selected for photosynthesis measurement. Two fully expanded leaves were measured in each tube and the two values were averaged as one replicate. Therefore, each data point in the figures represents the mean values of three replicates.