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Research article

Effects of phosphorus application on photosynthetic carbon and nitrogen metabolism, water use efficiency and growth of dwarf bamboo (*Fargesia rufa*) subjected to water deficit

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ABSTRACT

Dwarf bamboo (*Fargesia rufa* Yi), one of the staple foods for the endangered giant pandas, is highly susceptible to water deficit due to its shallow roots. In the face of climate change, maintenance and improvement in its productivity is very necessary for the management of the giant pandas' habitats. However, the regulatory mechanisms underlying plant responses to water deficit are poorly known. To investigate the effects of P application on photosynthetic C and N metabolism, water use efficiency (WUE) and growth of dwarf bamboo under water deficit, a completely randomized design with two factors of two watering (well-watered and water-stressed) and two P regimes (with and without P fertilization) was arranged. P application hardly changed growth, net CO_2 assimilation rate (P_n) and WUE in well-watered plants but significantly increased relative growth rate (RGR) and P_n in water-stressed plants. The effect of P application on RGR under water stress was mostly associated with physiological adjustments rather than with differences in biomass allocation. P application maintained the balance of C metabolism in well-watered plants, but altered the proportion of nitrogenous compounds in N metabolism. By contrast, P application remarkably increased sucrose-metabolizing enzymes activities with an obvious decrease in sucrose content in water-stressed plants, suggesting an accelerated sucrose metabolism. Activation of nitrogen-metabolizing enzymes in water-stressed plants was attenuated after P application, thus slowing nitrate reduction and ammonium assimilation. P application hardly enlarged the phenotypic plasticity of dwarf bamboo in response to water in the short term. Generally, these examined traits of dwarf bamboo displayed weak or negligible responses to water-P interaction. In conclusion, P application could accelerate P_n and sucrose metabolism and slow N metabolism in water-stressed dwarf bamboo, and as a result improved RGR and alleviated damage from soil water deficit.

1. Introduction

Due to the potential effects of climate change on precipitation and temperature patterns, plants are often subjected to temporary periods of soil water deficit during their life cycle. Soil water deficit is the most common environmental stress factor limiting the growth, development, productivity and regeneration of plants worldwide (Liu et al., 2014). Within a certain threshold of soil water stress, most plants are able to express several stress-related genes, which lead to a series of remarkable changes in morphological and physio-biochemical traits to resist or adapt to adverse environments (Lawlor and Cornic, 2002; Sato et al., 2010). However, these changes may vary greatly depending on the plant species, stress

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Abbreviations: AGMR, aboveground mass ratios; AMY, amylase; C_i, intercelluar CO_2 concentration; F_v/F_m, maximum quantum efficiency of photosystem II; GDH, glutamate dehydrogenase; GOGAT, glutamate synthase; GOT, glutamic-oxaloacetic transaminase; GPT, glutamic-pyruvic transaminase; G_s, stomatal conductance; GS, glutamine synthetase; INV, invertase; LMR, leaf mass ratios; LRWC, leaf relative water content; NH_4^+, ammonium; NiR, nitrite reductase; NO_2^-, nitrite; NO_3^-, nitrate; NR, nitrate reductase; NSC, non-structural carbohydrate; P_i, orthophosphate; P_n, net CO_2 assimilation rate; RGR, relative growth rate; RMR, root mass ratios; SMR, stem mass ratios; SPS, sucrose phosphate synthase; SS, sucrose synthase; WUE, water use efficiency; WUE_{intr}, intrinsic water use efficiency.

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duration and intensity, as well as soil conditions (Reddy et al., 2004).

Phosphorus is one of 17 essential nutrients required for plant growth, accounting for about 0.2% of a plant's dry weight. In general, more than 80% of the total amount of P in the soil is immobile and unavailable (e.g. Ca–P, Fe–P, Mg–P, Al–P and organic-P) (Suriyagoda et al., 2011). P can be readily absorbed by plants in the orthophosphate (P_i) forms (HPO_4^{2-} and $H_2PO_4^-$), which occur in soil solutions at very low concentrations (<10 μM). Most soils, even fertile types, are deficient in P_i as its uptake via root absorption is faster than its replenishment in soil solutions (Suriyagoda et al., 2011). Recent studies have demonstrated that P deficiency inhibits processes related to energy metabolism and biochemical synthesis, such as photosynthesis, respiration (especially the glycolytic pathway) and N fixation; P deficiency also reduces the activities of key enzymes involved in C and N metabolism (Burman et al., 2004; dos Santos et al., 2004; Burman et al., 2009). Moreover, P deficiency causes aberrant root architecture in terms of number and density of lateral roots, and thus affects P_i transport, which serves as a long-distance signal (Lin et al., 2014). Consequently, P is considered the most important element limiting plant growth.

Increasing water deficit significantly decreases P and water availability in soils (Suriyagoda et al., 2014), which further aggravates the difficulty of their utilization. This situation inevitably induces metabolic disorders and eventually results in serious reduction in productivity (Singh et al., 2006a). P fertilization not only alleviates the scarcity of available P in the soil but also improves plant stress tolerance (Cortina et al., 2013). A number of studies have shown that P-fertilized plants under water stress conditions exhibit enhanced root growth potential, xylem hydraulic conductivity and water use efficiency (WUE) (Jones et al., 2005). Other studies have also indicated that P application can affect dry matter partitioning because plants invest relatively less C and N into roots and more into leaves, which can increase the rates of leaf relative growth and CO_2 assimilation per unit of leaf area, as well as carbohydrate contents (e.g. sucrose, soluble sugar and starch) (dos Santos et al., 2004; Burman et al., 2009). In addition, P fertilization can accelerate nitrate (NO_3^-) reduction and ammonium (NH_4^+) assimilation and produce more nitrogenous compounds in water-stressed plants by promoting NO_3^- absorption and activation of enzymes (e.g. nitrate reductase, NR; glutamine synthetase, GS and glutamate synthase, GOGAT) (Burman et al., 2004; Garg et al., 2004). Finally, the adaptive changes of C and N metabolism induced by P fertilization are beneficial for plant survival and growth in drought-prone environments (Burman et al., 2004).

Several studies have analyzed possible regulatory mechanisms behind the effect of P application on drought response in plants. However, no comprehensive understanding exists from the viewpoint of C and N metabolism. Meanwhile, these studies are concentrated in a number of herbaceous and woody species, but did not focus on bamboo species, a semi-woody plant that is widespread all around the world. Weih (2001) showed evidence that fast-growing plant species are more sensitive to water and nutrient stress than slow-growing ones. Dwarf bamboo (*Fargesia rufa* Yi), one of the staple foods of the endangered giant pandas, is a dominant understory under a mixed of canopy of the evergreen *Abies fargesii* var. *faxoniana* and deciduous *Betula utilis* in subalpine zone, China. However, dwarf bamboo is highly susceptible to water stress due to its shallow roots (Liu et al., 2014). Given its fast-growing trait, dwarf bamboo makes soil P-deficient, which adversely affects subsequent seedling regeneration after mass flowering. Therefore, water and nutrient are the two determining factors for dwarf bamboo growth and yield. Maintenance and improvement in the productivity of dwarf bamboo will be an essential issue for the giant panda's survival and conservation in water deficit environments.

This study was designed to investigate how P application regulates photosynthetic C and N metabolism and WUE of dwarf bamboo under different water conditions to improve its growth, and whether the morphological and physio-biochemical traits are affected by the combined factors. To answer these questions, we investigated plant growth, water status, gas exchange and chlorophyll fluorescence parameters, levels of key compounds and enzymes activities involved in C and N metabolism. Also, we assessed phenotypic plasticity by using the above morphological and physio-biochemical traits.

2. Materials and methods

2.1. Plant material, growth conditions and experimental design

The experiment was carried out at Maoxian Mountain Ecosystem Research Station (103°53′E, 31°41′N, 1826 m), Chinese Academy of Sciences in southwestern China. On March 2013, the uniform and healthy plants (2 years old) of dwarf bamboo were obtained from the seedling nursery at Wanglang National Nature Reserve (103°55′ E, 32°49′ N, 2300 m) and then transplanted into 50 L plastic pots filled with 25 kg of homogenized topsoil from the experimental site. Each pot had one standard plant including 4–5 ramets. All plants were grown in a naturally lit greenhouse under a semi-controlled environment with a temperature range of 18–32 °C and relative humidity of 50%–85%, and irrigated regularly with water from a nearby stream. Prior to the treatments, total P (0.67 g kg^{-1}) and available P (5.1 mg kg^{-1}) in soils were first determined. About 4 months after the transplanting, the treatments, a completely randomized design with two factors of two water regimes and two P fertilization level, were applied for 45 days. Sixty standard plants were randomly allocated to all 4 combinations of water and P in the trial. The pots were weighed every other day and rewatered to 80%–85% (well-watered) and 30%–35% (water-stressed) relative soil water content by replacing the amount of transpired water. The two P fertilization treatments were without fertilization (no fertilizer supplied to plants) and with fertilization (6 g of calcium superphosphate containing 16% P_2O_5 supplied to each plant every 15 days). The amount of P application was determined by the highest concentration of available P loss from bamboo soil (Chen et al., 2011). To avoid systematic error caused by the possible differences in fluctuating environmental condition, all pots were rotated every five days during the experiment. In each treatment, three replicates, each including five plants, were used. Plant samples were collected at the end of the experiment.

2.2. Growth analysis

All plants were individually harvested and separated into leaves, stems and roots at the end of the experiment. The plant parts were washed, oven-dried at 70 °C for 72 h, and weighed. On the basis of these data, leaf mass ratios (LMR), stem mass ratios (SMR), root mass ratios (RMR) and aboveground mass ratios (AGMR) were obtained. The relative growth rate in terms of aboveground biomass (RGR) for each standard plant was calculated as $(\ln W_2 - \ln W_1)/(t_2 - t_1)$, where W_2 is the final biomass, W_1 is the initial biomass, and $t_2 - t_1$ is the time interval (days), respectively.

2.3. Leaf relative water content

Leaf relative water content (LRWC) was calculated according to the following formula: LRWC (%) = [(FW−DW)/(TW−DW)] × 100. Here, FW is the fresh weight, DW is the dry weight after drying at