



Original article

Positive effects of night warming on physiology of coniferous trees in late growing season: Leaf and root

Bo Tang^{a, b}, Chunying Yin^{a, *}, Yujie Wang^c, Yuyu Sun^{a, b}, Qing Liu^a^a Key Laboratory of Mountain Ecological Restoration and Bioresource Utilization & Ecological Restoration Biodiversity Conservation Key Laboratory of Sichuan Province, Chengdu Institute of Biology, Chinese Academy of Sciences, P.O. Box 416, Chengdu 610041, PR China^b University of Chinese Academy of Sciences, No. 19A Yuquan Road, Beijing 100049, PR China^c UNC Gillings School of Global Public Health, 135 Dauer Drive, Chapel Hill, NC 27599, USA

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ABSTRACT

Previous studies about the effects of experimental warming on tree species have focused primarily on response of morphology and physiology in leaf and biomass allocation in the growing season, and a few studies considered the importance of roots. Based on the available evidence, it is unclear whether photosynthesis rate is enhanced by night warming in late autumn an issue that deserves further investigation. Thus, we exposed two coniferous species, *Picea asperata* and *Abies faxoniana*, to night warming continued throughout the year to investigate morphological and physiological responses of roots and leaves in the autumn. The results showed that night warming caused significant increases in net influxes of NH_4^+ and NO_3^- in *P. asperata* seedlings corresponding well with net H^+ efflux and net influx of O_2 . Meanwhile, night warming had a positive effect on foliar gas exchange such as net photosynthesis rate, apparent quantum efficiency, dark respiration rate and maximum quantum efficiency of PS II, and nitrate reductase activity of roots. Additionally, root morphology such as total roots length, surface area, specific root area and specific root length was also stimulated by night warming. In contrast, night warming decreased concentrations of non-structural carbohydrate in leaves and roots of both species in autumn. The present study demonstrates that night warming would enhance late autumn leaf photosynthetic rate, and increase N uptake capacity of roots.

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1. Introduction

There is an overall trend of climate warming at the global scale, with more pronounced warming in the higher latitudinal and altitudinal regions (IPCC, 2013). Consequently, a cascade of studies have investigated plants responses to global warming (Lemmens et al., 2006; Vicca et al., 2007; Danby and Hik, 2007; Leppalammi et al., 2013; Zheng et al., 2013), such as structure, physiology and function of leaves (Jin et al., 2011; Zheng et al., 2013), root lifespan

and physiology (Bai et al., 2012; Yin et al., 2014), plant phenology (Körner and Basler, 2010) and carbon gain (Gimeno et al., 2012) as well as net primary productivity (Hudson and Henry, 2009). It is reported that globally averaged maximum and minimum temperatures have both increased since 1950 (IPCC, 2013), which tends to affect carbon assimilation and consumptions in plants, because photosynthesis in most plants occurs during the daytime and is more sensitive to daily maximum temperature, whereas plants respiration occurs throughout the whole day (Atkin et al., 2013), and is therefore influenced by both daily maximum and minimum temperature (Peng et al., 2013). To our knowledge, a great deal of attention has been focused primarily on continuous warming or day warming (Zhao and Liu, 2009; Zheng et al., 2013), while little is known about the effect of night warming on trees, especially on their root N uptake rates.

It has been widely recognized that effects of global warming on plants varied by season, meteorologic conditions, phenology and plant organs (Gimeno et al., 2012; Yin et al., 2013, 2014). Alteration in plant phenology is one of the most sensitive and observable

Abbreviations: AQE, apparent quantum efficiency; Fv/Fm, maximum quantum efficiency of PS II; NR, nitrate reductase; NSC, non-structural carbohydrate; PAR, photosynthetically active radiation; P_{max} , light-saturated rate of photosynthesis; P_n , net photosynthesis rate; R_d , dark respiration rate; SLA, specific leaf area; SRA, root specific surface area; SRL, specific root length; TF, triphenylformazan; TTC, triphenyltetrazolium chloride.

* Corresponding author. Chengdu Institute of Biology, Chinese Academy of Sciences, P.O. Box 416, Chengdu 610041, PR China.

E-mail address: yincy@cib.ac.cn (C. Yin).

biological response to global warming (Bronson et al., 2009; Morin et al., 2010; Polgar and Primack, 2011). Some field (Rollinson and Kaye, 2012) and modeling studies (Lebourgeois et al., 2010) have illuminated that warm temperature would expand plant growing season due to early onset and later end (Parmentier et al., 2011; Chung et al., 2013). Previous studies about the effect of experimental warming on tree species have focused primarily on net mineralization, net nitrification and denitrification rates, ectomycorrhizal colonization and root exudation in early growing season, peak of growing season and non-growing season (Zhao and Liu, 2009; Yin et al., 2012, 2013, 2014). Global warming affects plant growth through direct effects on photosynthesis and respiration (Albert et al., 2011) and indirect effects on soil nitrogen availability (Sardans et al., 2008) and soil moisture (Holsten et al., 2009). Previous study reported that an increase in autumn temperature did not increase the photosynthetic rate but affects the consumption of excess energy in seedlings of Jack pine (Busch et al., 2007). Based on the available evidence, it is unclear whether photosynthesis rate is enhanced by warming at the late autumn (Lebourgeois et al., 2010; Gimeno et al., 2012), and it deserves further investigation.

It is well known that fine roots of plants play a key role in the acquisition of water and essential nutrients, which make a substantial contribution to biogeochemical cycling at the ecosystem level, and soil resources available for plants are highly variable in space and time (Pregitzer et al., 2002). Plants must respond to the rapid changes in soil resource availability by physiological and structural adjustments of the fine absorbing roots, such as to increase the rate of nutrient uptake per unit root length (Ryel and Caldwell, 1998). Therefore, changes in physiological activity of roots under unstable circumstances would result in corresponding shifts in plant growth and root lifespan (Yin et al., 2014). Although many conifer species are adapted to cool, acidic soils, and are expected to absorb more ammonium in comparison with nitrate (Hawkins and Robbins, 2010), nitrate reductase (NR) is generally considered to be the rate-limiting enzyme in inorganic nitrogen (N) assimilation (Young et al., 2007; Yu and Zhang, 2012) because nitrogen absorption is directly associated with the reduction rate of nitrate to nitrite (Calatayud et al., 2008; Huang et al., 2013). Root activity (as TTC, triphenyltetrazolium chloride, reducing capacity) is commonly used as an important physiological parameter for evaluation of ion and water uptake (Huang et al., 1997; Wang et al., 2006). To date, a great deal of attention is being paid to the root exudation and soil nitrogen transformation under experimental warming (Yin et al., 2012, 2013). These studies reported that experimental warming marked increased exudation rates in *Picea asperata* and *Abies faxoniana*. Few studies, however, have investigated roots N uptake rates and their associated parameters under global warming.

A few studies have focused on plant growth and physiological response of *P. asperata* and *A. faxoniana* seedlings to short-term continuous warming (Yin et al., 2008; Zhao and Liu, 2009; Hou et al., 2011). However, long-term experiments to investigate the effects of artificial warming are definitely needed (Wang et al., 2011). Early developmental stages of plants are expected to be more sensitive to environmental changes than adult stages (Weltzin et al., 2000) and are critical life-stages of plant life cycles, which are tightly associated with modulating forest regeneration and species composition, as well as ecological succession (Lloret et al., 2004). Furthermore, most conifers keep their leaves year-around and are able to photosynthesize when temperatures are warm, the impact of an extended autumn due to warming would likely to be greater for conifer growth than for deciduous trees. Therefore, we used the seedlings of *P. asperata* and *A. faxoniana*, the dominant species of subalpine coniferous forests in the Eastern Tibetan Plateau located at the transition zone between Qinghai-

Tibet plateau and the Sichuan basin (Wang et al., 2003), as materials and investigated the morphological and physiological responses of leaf and root in the late autumn to investigate the effects of global warming on conifer trees. Based on the available information, we hypothesized that: 1) night warming would enhance late autumn leaf photosynthetic rate; 2) night warming would increase N uptake capacity of roots.

2. Materials and methods

2.1. Study site and experimental design

The study was conducted in Maoxian Mountain Ecological Research Station (31°42' N, 103°54' E, 1826 m a.s.l.), Chinese Academy of Sciences, Sichuan province, China, with mean annual temperature, precipitation and evaporation 9.3 °C, 825.2 mm, and 968.7 mm, respectively. In this region, the growing season generally starts in late April and ends in October (Zhu et al., 2012). The current experiment continued the study of Yin et al. (2014), which was designed as a randomized block experiment with two warming treatments (control and night warming) and two species (*P. asperata* and *A. faxoniana*). Each plot was 2 × 2 m in size with a 5 m distance between any two adjacent plots. Each treatment of each species had 4 plots as replicates. The indigenous soil of all plots was replaced, to a depth of 30 cm, by sieved topsoil from a nearby coniferous forest. The soil classified as a mountain brown soil series (Chinese taxonomy), and the soil properties, determined in October 2010, were as follows: pH, 6.8; total N, 4.0 g kg⁻¹; soil organic C, 61 g kg⁻¹; and bulk density, 0.91 g cm⁻³. The warmed plots were heated by MSR-2420 infrared radiators (Kalglo Electronics Inc, Bethlehem, PA, USA) while the control used 'dummy' heaters of the same shape and size as the infrared heater suspended 1.5 m above the middle of the plots. Uniform 4-year-old *P. asperata* and *A. faxoniana* seedlings from a local nursery were selected based on plant height and stem base diameter at the beginning of the experiment. The average plant height and stem basal diameter were 15.6 ± 0.8 cm and 3.7 ± 0.7 mm for *P. asperata*, and 11.8 ± 0.7 cm and 3.5 ± 0.6 mm for *A. faxoniana*, respectively. In each plot, the space between seedlings was 30 × 40 cm in the beginning and 70 × 80 cm since 2013. The experiment layout was conducted in September 2010 and warming treatment was initiated on October 2011, which was 13 months after the seedlings were planted. The warmed plots were heated from local time 7:00 pm to 7:00 am (12 h day⁻¹) year-around, and all the plots were watered with collected precipitation nearby and weeds were removed as frequently as needed.

Air temperature (at 5 cm aboveground) and soil temperature (at 5 cm depth) were measured using DS1923G temperature/humidity iButton data loggers and DS1921G Thermochron iButton data loggers (DS1921G-F5, Maxim Integrated Products; Dallas Semiconductor Inc., Sunnyvale, CA, USA) in each plot, respectively. Compared to the control plots (Yin et al., 2014), the half-hourly air temperature (at 5 cm aboveground) and soil temperature (at 5 cm depth) within the warmed plots elevated by an average of 1.95 °C and 3.10 °C, respectively. The soil water content was not significantly different ($P = 0.409$) between the warmed plots (25.4 ± 2.3%) and the control plots (26.2 ± 1.7%). Please refer to Yin et al. (2014) for further information about the microclimate of the experiment site.

2.2. Gas exchange and chlorophyll fluorescence

The fully expanded leaves, which were randomly selected from 3 plants of each species in each treatment, were measured for photosynthesis light response curve under controlled optimal

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