CO$_2$ elevation and soil warming reduce cold hardiness of jack pine under photoperiods of seed origin and latitudes of potential migration

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Abstract

Climate change is predicted to cause northward migration of boreal tree species. However, the success of such a migration will be determined by trees' ability to acclimate to the environmental conditions at the potential new site. This study was aimed to assess the interactive effects of changes in photoperiod associated with northward migration and soil warming on the ecophysiological traits of jack pine (*Pinus banksiana* Lamb.) under different carbon dioxide concentrations [CO$_2$]. We examined the responses of foliar gas exchange and seedling cold hardiness after exposing 1-year old seedlings to two [CO$_2$] (400 and 950 μmol mol^{-1}), two soil temperatures (growing season average at seed origin and 5 °C warmer) and three photoperiod regimes (seed origin, and 5° and 10° further north) for one growing season. We found that the CO$_2$ elevation significantly increased photosynthetic rate measured at treatment CO$_2$, photosynthetic water use efficiency, maximum rate of carboxylation and triose phosphate utilization. Some of the effects were modified by photoperiod. Furthermore, the CO$_2$ elevation and soil warming both reduced seedling cold hardiness, as indicated by increases in injury index. The lack of interactions between photoperiod and other treatments (elevated [CO$_2$] and soil temperature) suggests that young jack pine seedlings may have the ability to acclimate to the new photoperiod regimes at higher latitudes north of the seed origin.

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Introduction

Climate is changing rapidly. Other than increasing CO_2 and temperature levels, precipitation patterns and weather extremes are also expected to change (Cao and Caldeira 2010; IPCC 2013; Luthi et al. 2008). These changes will occur in a relatively short period of time so trees may have to rapidly acclimate or adapt to new conditions, or migrate to new locations, or a combination of both in order to preserve their populations (Aitken et al. 2008). Trees live longer than other plant forms and, therefore, their physiological plasticity to acclimate to the changing environment of their current location or the different environment of a new location is critical (Lambers and Oliveira 2019).

Elevated atmospheric $[CO_2]$ generally stimulates photosynthesis in C_3 plants with a concomitant increase in biomass (Eamus and Ceulemans 2001) but such a positive effect is often not sustained due to down regulation of photosynthetic capacity (Cui and Nobel 1994; Lambers and Oliveira 2019). In the meantime, stomatal conductance typically decreases under elevated $[CO_2]$ (Bunce 2004; Gunderson et al. 2002; Leakey et al. 2006; Marchi et al. 2004; Medlyn et al. 2001; Morgan et al. 2004).

Soil temperature is likely to increase under the predicted changes of climate in boreal forests where photosynthesis and tree growth are generally restricted by low soil temperatures (Aphalo et al. 2006; Ensminger et al. 2008). Changes in soil temperature influence morphological and physiological traits (Cai and Dang 2002; Newaz et al. 2016), such as stomatal conductance and water uptake (Alvarez-Uria and Körner 2007; Ambebe et al. 2010; Frechette et al. 2011; Zhang and Dang 2007), and development of cold hardiness (Dalen and Johnsen 2004; Lutze et al. 1998). Low soil temperature restricts nutrient and water uptake (Grossnickle 2000; Peng and Dang 2003; Stathers and Spittlehouse 1990) and retards establishment and early growth of newly planted seedlings (Grossnickle 2000; Smith 1985). Soil temperature can also interact with air temperature in affecting the ecophysiological traits of trees, for example, the beneficial effects of increased soil temperature may be offset by increases in vapor pressure deficit and transpiration rate associated with a concurrent increase in air temperature (Domec et al. 2009).

In response to changing climate, trees are expected to migrate northward (Bunnell and Kremsater 2012), either naturally or with human assistance. As the predicted shifts of climate envelopes are substantial for many North American species (McKenney et al. 2007, 2011), trees would face quite different environments from their current habitats on their way north, for example, photoperiod getting longer in the summer and shorter in the winter and a faster transition between seasons. This photoperiod change may have significant implications for plant phenology and physiological processes (Lambers and Oliveira 2019; Pothier and Prevost 2002). A possible consequence may include the desynchronization in seasonal cold hardiness and bud phenology development, leading to increasing risks of cold damage (Augspurger 2013; Gu et al. 2008; Li et al. 2015; Man et al. 2009).

The effects of individual environmental factors on boreal trees, such as temperature and photoperiod, are well documented (DeLucia and Smith 1987; Fraser 1962; Li et al. 2015; Peng and Dang 2003; Soolanayakanahally et al. 2013; Way and Sage 2008a, b). Comparatively, interactive effects are less studied but can be quite different from individual effects (Curtis et al. 2000; Nowak et al. 2004). For example, the stimulation of elevated $[CO_2]$ to photosynthesis can decrease with decreasing light (Allen et al. 1990) but the relative stimulation to biomass may increase with decreases in light condition (Marfo and Dang 2009) and the ecophysiological mechanisms of response to elevated CO_2 change with light conditions (Dang et al. 2020a, b). The ecophysiological response to the interactions of elevated

CO_2 and nutrient supply varies with species (Dang et al. 2020b). Elevated $[CO_2]$ reduces the negative impact of drought stress (Mishra et al. 1999) and the response can be altered by photoperiod (Inoue et al. 2020).

Jack pine (*Pinus banksiana* Lamb.) is a conifer tree species of great ecological and economic importance and the second most planted tree species in Canada (Forestry Canada 1992). Jack pine represents about 37% of the total annual softwood harvest volume in Ontario (OMNR 1991). It grows in a wide range of climatic conditions (Rudolf 1965). Despite of its high levels of genetic diversity, the distribution and productivity of jack pine will be affected by climate change (Colombo et al. 2007). However, our knowledge how jack pine may respond to climate change and changes in environmental conditions associated with a potential northward migration is still limited. Because of its great ecological and commercial values and sensitivity to climate change (Colombo et al. 2007; Newaz et al. 2016; Rudolf 1965), such knowledge is particularly important for the development of proper adaptive strategies to sustain the distribution and productivity in the future. In this study, we assessed the physiological responses of jack pine to elevated $[CO_2]$ under different scenarios of soil warming and northward migration. Although the interactive effects of $[CO_2]$ and soil temperature on jack pine have been examined previously (Zhang and Dang 2005, 2007), how the responses may vary with photoperiod are unknown. Since warmer soil temperature, elevated $[CO_2]$ and longer photoperiod all can increase photosynthesis, we hypothesize that the combination of warmer soil temperature, longer growing season photoperiod, and elevated $[CO_2]$ would enhance the physiological performance of jack pine; but a faster rate of decline in photoperiod during the cold hardening phase in the fall would hinder the proper development of cold hardiness because the trees would have less time to complete the cold hardening process.

Materials and methods

Plant materials

One-year old jack pine seedlings were obtained from the Boreal Tree Seedling Nursery near Thunder Bay. The seedlings were raised from seeds collected from Kakabeka region (48° 57′ N & 90° 44′ W). A total of 608 seedlings, relatively uniform in height and diameter (mean height 13.05 cm; mean root collar diameter 0.21 cm), were planted in pots of 15 cm in height and 13 cm in diameter filled up with a mixture of premium grade vermiculite and peat moss in a ratio of 1:1 (v/v).

Experimental design

The experiment was conducted in four green houses at Lakehead University's Thunder Bay campus following a split-split-plot design, with $[CO_2]$ as the whole plot, soil temperature as the sub-plot and photoperiod as the sub-sub plot. The treatments included two levels of $[CO_2]$ (400 and 950 $\mu mol \ mol^{-1}$), two soil temperatures (soil temperature at seed origin, and 5° C warmer) and three photoperiod regimes (photoperiod at seed origin, and 5° and 10° further north). Two levels of $[CO_2]$ were randomly assigned to four independent greenhouses with two replicates of each. The two levels of soil temperature were set up within each level of $[CO_2]$ and three levels of photoperiod were assigned within each soil temperature.

Environmental controls

The experiment was conducted between November 20, 2013 and May 31, 2014. The photoperiods in all the greenhouses were set the same that simulated the seasonal course from April 16 to October 31 for the location of the longest photoperiod treatment. The photoperiods for the shorter day treatments were achieved by manual shading at both ends of the day (Newaz et al. 2016). The temperatures in all the greenhouses simulated the seasonal course of the seed origin. The dates referred to hereafter are the simulated dates. The $[CO_2]$ in the greenhouses was elevated using electronic ignition natural gas CO_2 generators (model GEN-2E, Custom Automated Products Inc, Riverside, CA). Circulation fans were used to distribute CO_2 evenly throughout each of the greenhouses. The $[CO_2]$ in each greenhouse was monitored and controlled automatically with an Argus CO_2 Control System (Argus, Vancouver, BC, Canada). The levels of CO_2 in each treatment varied within ± 10 μmol mol^{-1} of the set point. The soil temperature of seed origin simulated the biweekly mean soil temperatures measured in 2012 and 2013 at the seed origin (Kakabeka region, Newaz et al. 2016). The soil temperatures were the averages of field measurements at 5 cm and 20 cm depth. Soil temperatures were controlled using the soil temperature control system designed by Cheng et al. (2000) and the settings were adjusted in synchronization with the adjustment of photoperiods. Bud setting time was defined as the number of days counted from September 16 (simulated) to the day when the setting of the terminal bud was completed. The simulated day length and day/night air temperature on September 16 were 12 h and 14 °C/8 °C, respectively. Photoperiods were extended using high-pressure sodium lamps when the natural day lengths were shorter than the set values or shortened through manual shading when the natural day lengths were longer than the set values. Seedlings were fertilized biweekly with 7.14 mmol N, 0.56 mmol P and 2.12 mmol K per litre of water during the rapid growth phase and 1.78 mmol N, 2.20 mmol P and 4.64 mmol K per liter of water during the hardening phase (Scarratt 1986). The soil moisture level was monitored using a Delta-T ML2x probe and HH2 moisture meter (Delta-T Devices, Cambridge, UK) and maintained at 60–70% of the field water capacity. In all greenhouses relative humidity was maintained at 55–60% during the rapid growth phase and 45–50% during the hardening phase. The day and night air temperatures were controlled to mimic the mean biweekly day and night air temperatures at the seed origin. Relative humidity and air temperature were controlled automatically using the Argus Control System referred to previously.

Gas exchange measurements

Foliar gas exchange was measured on three randomly selected seedlings of each treatment combination in the middle of the simulated summer (102th–112th day of treatment) when the seedlings were in the rapid growing stage (Newaz et al. 2016). All measurements were made between 09:30 A.M. and 2:30 P.M. The measurements were made on current foliage using a PP-Systems CIRAS-3 open gas exchange system (PP System Inc., Amesbury, MA, USA). Photosynthetic responses to CO_2 concentration (A/C_i curves) were measured at 50, 150, 250, 400, 550, 730, 900 and 1200 μmol mol^{-1} CO_2, at photosynthetically active radiation of 800 μmol m^{-2} s^{-1}, 25 °C air temperature and 50% relative humidity. The net rate of carbon dioxide assimilation (A_n), stomatal conductance (g_s) and transpiration rate (E) were calculated according to Farquhar

et al. ([1980](#)). Water use efficiency (*WUE*) was calculated as A_n/E for each measurement. The A/C_i response curves were analyzed to estimate the maximum rate of carboxylation (V_{cmax}), maximum rate of electron transport (J_{max}), triose phosphate utilization (*TPU*) and other relevant parameters according to Sharkey et al. ([2007](#)). The light saturated (PAR 800 μmol m^{-2}s^{-1}) A_n measured at the growth [CO_2] (400 and 950 μmol mol^{-1}) and at the ambient [CO_2] for both CO_2 treatments (A_{n-400}) were derived from the *A/Ci* curves. g_s, *E* and *WUE* measured at the corresponding growth [CO_2] were used in data analyses. The needles used in foliar gas exchange measurements were collected and the projected leaf area was determined using the Regent WinSeedle system (Regent Instruments Inc, Quebec, Canada). To avoid the impact of needle removal for leaf area measurement on growth and physiology, seedlings used in foliar gas exchange measurement were not used in any other measurements.

Electrical conductivity and index of injury

The cold hardening phase was started in mid-April (mimicking the environment of mid-September) with day length and day and night air temperature at 12 h and 14 °C and 8 °C, respectively, and continued until the end of May (mimicking end of October) with day length and day and night air temperature of 10 h and 7 °C and 2 °C, respectively. The cold hardiness of shoot tips was assessed when growth had stopped and buds were set (Newaz et al. [2016](#)) following the method by Colombo et al. ([1989](#)). Terminal shoot tips of 3 cm in length were collected from nine seedlings randomly selected from each treatment combination and divided among three testing temperatures (-5, -15 and -30 °C). Each shoot tip was rinsed with distilled water and placed in a test tube containing 15 ml distilled water and allowed to incubate at room temperature (20–25 °C) for 24 h. After a vigorous shaking of the test tubes, the control electrical conductivity (ECC) of the bathing solution was determined using a Fisher Accumet AR 29 electrical conductivity meter (Fisher Scientific, Ottawa, Canada). The bathing solution was then separated and the wet shoot tips in stoppered test tubes were cooled down to each testing temperature at a rate of 5 °C per hour using a programmable freezer (Foster Refrigeration Ltd., King's Lynn Norfolk, U.K.). After 70 min at the testing temperature, the temperature inside the freezer was gradually raised (5 °C per hour) to room temperature and the samples were transferred to an insulated box at 5 °C and left overnight. The previously separated bathing solution was returned to the corresponding test tubes, which were incubated for 24 h at room temperature. At this stage, electrical conductivity of the bathing solutions was measured again as the freezing electrical conductivity (ECF). The samples were then placed in a drying oven at 80 °C for 2 h to kill the tissues and left in room temperature for another 24 h. The electrical conductivity of the post-killing bathing solution was measured (ECK).

The index of injury (I_i), which is inversely related to cold hardiness (Flint et al. [1967](#)), was calculated as follows (Colombo et al. [1989](#)):

$$I_i = \frac{\frac{ECF}{ECK} - \frac{ECC}{ECK}}{1 - \frac{ECC}{ECK}} \times 100$$

where I_i = index of injury (%), ECC = control electrical conductivity, ECF = electrical conductivity of the bathing solution measured following freezing of the shoot tips, and ECK = electrical conductivity of the bathing solution measured after killing the shoot tips.

Statistical analysis

All data were subjected to Analysis of Variance (ANOVA). Shapiro–Wilk and Bartlett tests were conducted to check for normality of distribution and homogeneity of variance, respectively. The J_{max}, TPU and R_d data were transformed using natural logarithm function, g_s using square root and WUE using reciprocal of square root to meet the ANOVA assumptions. Tukey's HSD Post-hoc comparisons were carried out when ANOVA tests showed significant treatment effects or interactions ($P \leq 0.05$). In the analyses, [CO_2], soil temperature and photoperiod were treated as fixed variables. All analyses were done using R 3.5.0 (R Development Core Team 2018).

Results

Gas exchange

While the net CO_2 assimilation rate at ambient [CO_2] (A_{n-400}) was not affected by any of the treatments or their interactions (Table 1), the net CO_2 assimilation rate at growth [CO_2] ($A_{n-growth}$) was significantly higher at elevated [CO_2] (Fig. 1a). The photosynthetic water-use efficiency (WUE) was significantly higher at elevated [CO_2] (Fig. 1b). The maximum rate of carboxylation (V_{cmax}) tended to increase with increasing photoperiod under the ambient [CO_2] but the differences between different photoperiod

Table 1 ANOVA P-values for the effects of carbon dioxide concentration (C), soil temperature (ST), photoperiod (PP) and their interactions on net photosynthetic rates measured at a common [CO_2] (A_{n-400}) and corresponding growth [CO_2] ($A_{n-growth}$), stomatal conductance (g_s), transpiration rate (E), photosynthetic water-use efficiency (WUE), maximum rate of carboxylation (V_{cmax}), light saturated rate of electron transport (J_{max}), triose phosphate utilization (TPU), day time dark respiration (R_d) and index of injury (I_i) at test temperatures of -5, -15 and -30 °C in jack pine seedlings

Response variables	Treatment effects						
	C	ST	PP	C * ST	C * PP	ST * PP	C * ST * PP
An-400	0.300	0.113	0.896	0.937	0.825	0.908	0.844
An-growth	**0.013**	0.938	0.865	0.342	0.853	0.465	0.424
g_s	0.234	0.691	0.603	0.905	0.366	0.453	0.862
E	0.131	0.599	0.709	0.722	0.699	0.530	0.838
WUE	**0.010**	0.416	0.916	0.756	0.366	0.887	0.905
V_{cmax}	**0.003**	0.067	**0.004**	0.764	**0.006**	0.649	0.343
J_{max}	0.079	0.948	0.335	0.433	0.616	0.727	0.087
TPU	**0.038**	0.706	0.552	0.457	0.697	0.379	**0.031**
R_d	0.391	0.365	0.518	0.818	0.746	0.883	0.078
I_i at -5 degree	**0.025**	0.201	0.471	0.273	0.466	0.775	0.167
I_i at -15 degree	**0.028**	**0.020**	0.727	0.235	0.403	0.840	0.650
I_i at -30 degree	**0.010**	**0.047**	0.513	0.710	0.477	0.718	0.756

Seedlings were grown under two levels of [CO_2] (400 and 950 µmol mol^{-1}), two soil temperature (average temperature at seed origin and 5 °C warmer) and three photoperiod regimes (photoperiod at seed origin, and 5° and 10° further north). Values in bold are significant at 0.05
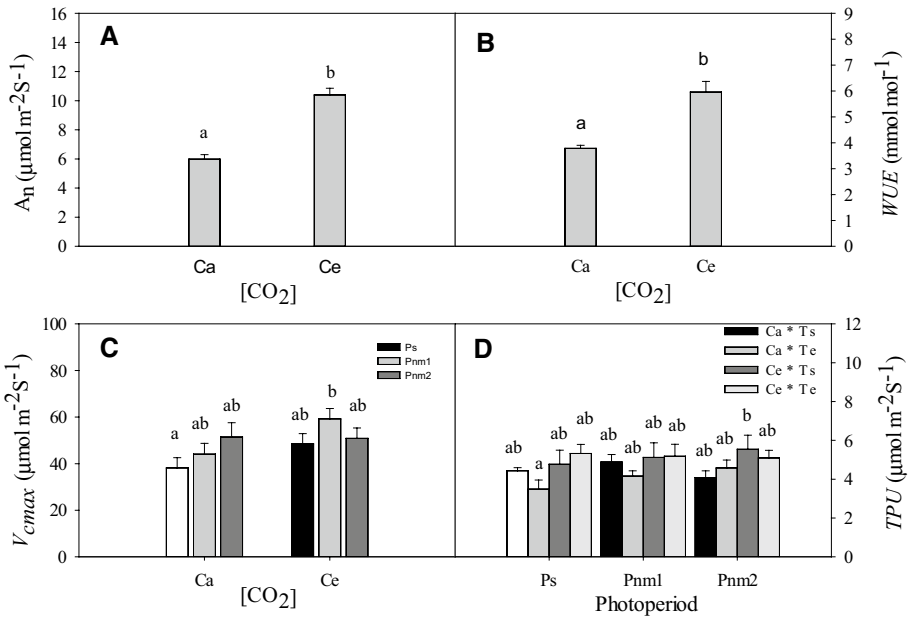
Fig. 1 Mean ($\pm$SE) net photosynthetic rate at growth CO_2 ($A_{n\text{-}growth}$), photosynthetic water-use efficiency (*WUE*), maximum rate of carboxylation (V_{cmax}) and triose phosphate utilization (*TPU*) in jack pine seedlings grown under two levels of $[CO_2]$ (Ca = 400 and Ce = 950 μmol mol^{-1}), two soil temperatures (Ts = seed origin and Te = 5 °C warmer) and three photoperiod regimes (Ps = seed origin, and Pnm1, Pnm2 = 5° and 10° further north). Means with different letters within the same graph were significantly different from each other (p ≤ 0.05)

treatments were not statistically significantly; under elevated $[CO_2]$, in contrast, V_{cmax} was highest at the intermediate photoperiod but the differences between photoperiods were again not statistically significant (Fig. 1c, Table 1). V_{cmax} was not significantly different between the two CO_2 treatments under the same photoperiod regime despite the significant interaction between CO_2 and photoperiod (Fig. 1c, Table 1). Although the triose phosphate utilization (*TPU*) was generally greater with elevated $[CO_2]$, the differences varied with soil temperature and photoperiod regime (significant 3-way interaction) (Fig. 1d, Table 1). However, the treatments or their interactions had no significant effect either on stomatal conductance (g_s) or on transpiration rate (*E*) (Table 1). Elevated $[CO_2]$ marginally increased the light saturated rate of electron transport (J_{max}) (P = 0.079, Table 1).

Index of injury

The index of injury (I_i) was significantly higher with elevated $[CO_2]$ at all three testing temperatures (Fig. 2a–c). I_i increased with elevated soil temperature at testing temperatures − 15 and − 30 °C (Fig. 2d, e) but was not affected by photoperiod or any treatment interaction (Table 1).
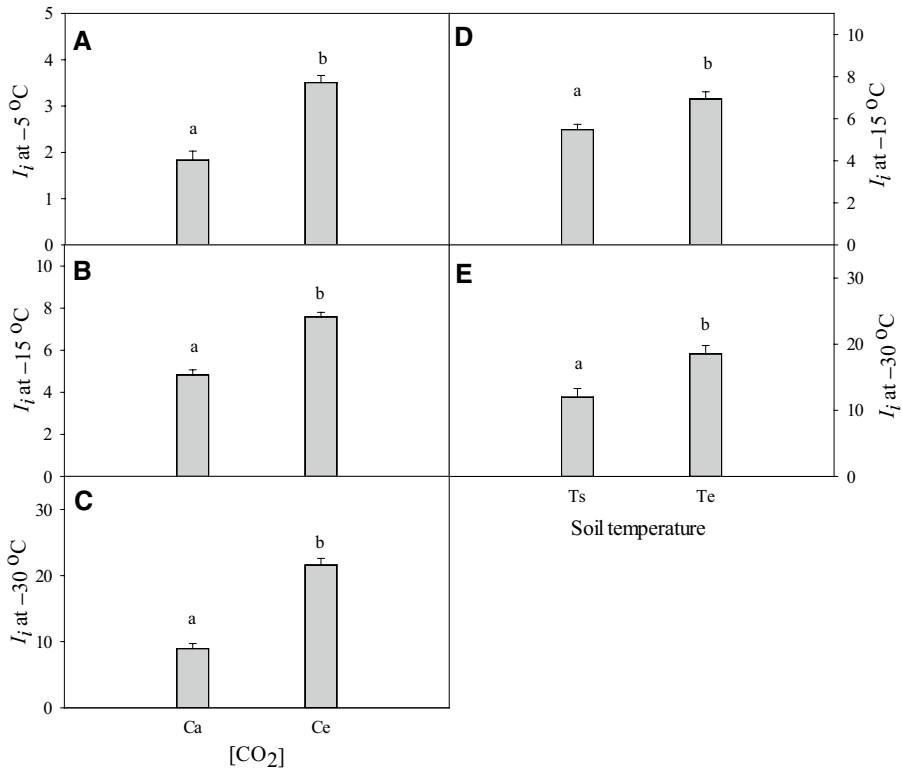
Fig. 2 Index of injury (I_i, mean ± SE) at −5, −15 and −30 °C in jack pine seedlings. Seedlings were grown under two levels of [CO_2] (Ca = 400 and Ce = 950 μmol mol⁻¹), two soil temperatures (Ts = seed origin and Te = 5 °C warmer) and three photoperiod regimes (Ps = seed origin, and Pnm1, Pnm2 = 5° and 10° further north). For each graph, means with different letters were significantly different from each other (p ≤ 0.05)

Discussion

The greater net photosynthetic rate ($A_{n\text{-}growth}$) under elevated atmospheric [CO_2] ('CO_2 fertilization effect') is consistent with the findings of Zhang and Dang (2005) on jack pine and white birch seedlings, Danyagri and Dang (2014a) on mountain maple, DeLucia and Thomas (2000) on four hardwood species and Tjoelker et al. (1998) on five boreal tree species including jack pine. The increase is probably due to the increased availability of substrate (CO_2) and enhanced photosynthetic enzyme activity (Zhang and Dang 2006), as the CO_2 assimilation in C_3 plants is not CO_2-saturated at current CO_2 level (Lambers and Oliveira 2019). The seedlings in all treatment combinations were well-fertilized and therefore the effects of elevated [CO_2] were unlikely limited by nutrient availability. The improved photosynthetic water-use efficiency (*WUE*) under elevated [CO_2] was also consistent with the results of other studies (Keenan et al. 2013; Long et al. 2004; Zhang and Dang 2005) and was likely primarily resulted from reduced stomatal conductance (Bunce 2004; Gunderson et al. 2002; Leakey et al. 2006; Medlyn et al. 2001) as reductions in stomatal conductance have greater negative impact on transpiration than on photosynthesis, leading to an increase of the photosynthesis–transpiration ratio (Lambers and Oliveira

2019). However, decreases in leaf area to root mass ratio or leaf mass ratio may also be a contributing factor (Norby and O'Neill 1991; Poorter 1999; Newaz et al. 2017).

The lack of photosynthetic down-regulation in this study is consistent with the observations by Osborne et al. (1997), Liang et al. (2001), Zhang and Dang (2006), Darbah et al. (2010), and Danyagri and Dang (2014b), but different from those by Ellsworth et al. (2004), Lewis et al. (2004), Nowak et al. (2004), Tissue and Lewis (2010) and Watanabe et al. (2011). Photosynthetic down-regulations are usually associated with nutrient restriction or reduced sink strength (Jach and Ceulemans 1999; Lambers and Oliveira 2019). In this study, jack pine seedlings were well fertilized and had a strong sink as shown by high TPU under elevated $[CO_2]$ (Hicklenton and Jolliffe 1980; Koch et al. 1986; Peet et al. 1986; Porter and Grodzinski 1984). The stimulated photosynthesis at elevated $[CO_2]$, however, may not be maintained for long due to feedback within plants and ecosystem (Luo and Reynolds 1999), as well as the change of sink activity with developmental stage and leaf age (Long et al. 2004).

Elevated $[CO_2]$ and warmer soil temperature both reduced the cold hardiness of jack pine seedlings, which is consistent with the findings of other studies (Barker et al. 2005; Guak et al. 1998; Lutze et al. 1998; Repo et al. 1996). The cold hardiness in all the treatments was between -15 °C and -30 °C, as indicated by the index of injury values (Colombo et al. 1989). Our previous study has shown that elevated $[CO_2]$ and warmer soil temperature both increased the growth of those seedlings (Newaz et al. 2016). The trade off between increased growth and reduced cold hardiness is also reported for other species (Dalen and Johnsen 2004). The reduction in cold hardiness may be related to reduced carbohydrate availability (Ögren et al. 1997) due to higher rates of root respiration under warmer soil temperatures (Ögren et al. 1997; Repo et al. 2004), or higher temperatures for ice nucleation under elevated $[CO_2]$ (Lutze et al. 1998). Soil temperature and $[CO_2]$ levels also affect membrane fluidity, calcium influx to the cytosol, xylem sap pH, and ABA concentration, which would all influence cold hardiness development (Hwei-Hwang et al. 1983; Monroy and Dhindsa 1995). The lack of photoperiod and interaction effects on cold hardiness in jack pine seedlings may suggest that the earlier and faster decline in photoperiod at higher latitudes may have promoted both growth cessation and bud set (Newaz et al. 2016). Our results suggest that there may be considerable risks associated with transferring jack pine seeds to higher latitudes according to the projected shifts of its climate envelope or niche because trees may suffer substantial frost damages due to reductions in cold hardiness. However, our results shed no light on the effects of the rate of air temperature declines in the fall on the development of cold hardiness (Bigras et al. 2001) because all the seedlings in the study were exposed to the same air temperature regime. Synchronized changes in air temperature and photoperiod and their interactions with other environmental factors may play a critical role in regulating the process of cold hardiness development. Therefore, studies to better understand the interacting effects of soil temperature, air temperature, photoperiod regime and $[CO_2]$ are imperative before any reliable adaptive policy or strategy can be made.

The findings of this study suggest that elevated atmospheric $[CO_2]$ accelerated physiological processes, however, both elevated $[CO_2]$ and warmer soil temperature retarded cold hardiness in young jack pine seedlings. The lack of significant photoperiod effects or significant interactions with $[CO_2]$ or soil temperature indicates that the effects of elevated $[CO_2]$ and soil temperature on physiological processes and cold hardiness may not change with changes in photoperiod regimes associated with northward migration under predicted responses to climate change, which does not support our hypothesis on possible changes in cold hardiness due to photoperiod. The significant negative effects of elevated $[CO_2]$ and

warmer soil temperature on cold hardiness found in this study suggest that forest managers should pay special attention to the cold hardiness of jack pine even when managing the species at its current location, particularly when transferring jack pine seeds to higher latitudes. Given the long rotation time of trees and the continued increases in atmospheric [CO$_2$] and temperature, our results suggest that trees may become more vulnerable to frost damage in the future. However, this study was carried out on 1-year-old tree seedlings under controlled environmental conditions. The responses of trees tend to change with age and size and other environmental conditions. Therefore, investigations on older trees and under field conditions are warranted for the development of proper adaptive strategies in forest management.

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