



Stem cycle analyses help decipher the nonlinear response of trees to concurrent warming and drought

Lorena Balducci¹ · Annie Deslauriers¹ · Sergio Rossi¹ · Alessio Giovannelli²

Received: 5 April 2019 / Accepted: 25 July 2019 / Published online: 22 August 2019
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Abstract

• **Key message** High-resolution analysis of stem radius variation can quantify the impact of warming and drought on stem water balance and stem growth in black spruce [*Picea mariana* (Mill.) B.S.P.]. Drought affected plant water status and stem growth. However, warming affects the components of the circadian stem cycle differently if the impacts occur in the daytime or nighttime. The interactive effect of abiotic stresses had less impact on the circadian stem cycle than when the stresses occurred independently.

• **Context** Warming and recent droughts in boreal regions reflect the multiple dimensions of climate change. How these climate-related stresses will affect the stem growth of trees remains to be described. Plant water relations can detect the dynamics of stem depletion and replenishment under conditions of climate-forced stress.

• **Aims** This study aimed to verify the impacts of a combination of asynchronous warming (nighttime versus daytime warming) and drought on stem water balance and stem growth in black spruce [*Picea mariana* (Mill.) B.S.P.].

• **Methods** We investigated the water status and variations in stem radius of black spruce saplings growing in a controlled environment from May through August. We grew four-year-old saplings in warmer conditions either during the day (DW) or night (NW) at temperatures ca. 6 °C warmer than the ambient air temperature (CT). We then simulated a one-month drought in June. Automatic point dendrometers provided a high-resolution analysis of variations in stem radius, and we also monitored leaf water potentials and volumetric soil water content during the entire experimental period.

• **Results** We detected significant reductions in stem radius variation under water deficit conditions. In the daytime warming scenario, we observed a significant increase in the duration of contraction and a decrease in expansion of the stems. The amplitude of this contraction and expansion was reduced under the nighttime warming conditions. The main effect of warming was to enhance drought stress by accelerating soil water depletion. Changes in predawn water potential drove the duration of stem circadian cycles under conditions of daytime warming, whereas irreversible growth dynamics drove these cycles under nighttime warming conditions due to the midday water potential. The interaction of night/daytime asynchronous warming and drought reduced the amplitude rather than the duration of stem contraction and expansion.

Handling Editor: Erwin Dreyer

Contribution of the co-authors A.D., A.G., and S.R. planned the research. L.B. performed measurements and analyzed the data with advices from A.G., S.R., and A.D. L.B wrote the manuscript with the contribution of all authors.

This article is part of the topical collection on *Wood formation and tree adaptation to climate*

✉ Lorena Balducci
Lorena1_Balducci@uqac.ca

Annie Deslauriers
Annie_Deslauriers@uqac.ca

Sergio Rossi
Sergio_Rossi@uqac.ca

Alessio Giovannelli
alessio.giovannelli@cnr.it

¹ Département des Sciences Fondamentales, Université du Québec à Chicoutimi, 555 Boulevard de l'Université, Chicoutimi QC, G7H2B1, Canada

² CNR-IRET, Istituto di Ricerca sugli Ecosistemi Terrestri, Via Madonna del Piano, 10, 50019 Sesto Fiorentino, Italy

• **Conclusion** Water deficit decreased stem growth during the growing season. Asymmetric warming (as a single independent treatment) affected the timing and magnitude of stem circadian cycles. Under daytime warming scenarios, the duration of contraction and expansion were regulated mainly by predawn water potential, inducing longer (shorter) durations of contraction (expansion). Under nighttime warming, the smaller amplitudes of stem contraction and expansion were associated with midday water potential. Therefore, the interaction of abiotic stresses had less of an impact on the circadian stem cycle components than when these stresses were applied independently.

Keywords Asynchronous warming · Water deficit · Point dendrometer · Water status · Saplings · Black spruce

1 Introduction

Global mean surface temperatures are expected to increase by 1.0–3.7 °C by 2100; however, this increase is projected to attain 4–5 °C for the boreal zone (IPCC 2014). Under this warming scenario, nighttime temperatures are to increase more than daytime temperatures (Casati and de Elia 2014; IPCC 2013). While the average annual frequency of warm nights and days is projected to increase in northern North America, it is expected that nighttime warming will be 10–50% greater than daytime warming (Sillmann et al. 2013). Boreal tree physiology and growth may respond differently to this asynchronous diurnal temperature increase than to uniform diurnal warming. Some studies have reported a positive effect of warming on growth and photosynthesis (Sage and Kubien 2007; Way and Oren 2010; Yamori et al. 2014). Tree response to warming includes nonlinear changes in stomatal control (Chaves et al. 2003), downregulation of leaf photochemistry when optimal thermal thresholds were exceeded (Ameje et al. 2012; Chaves et al. 2003), transitory growth increase (D'Arrigo et al. 2004), and increased water flux (Ellison et al. 2017). In the boreal forest, no significant climate-related decline in growth has been observed; however, some conifer species in eastern Canada impacted negatively by a rapid increase in summer temperatures of the previous year (Girardin et al. 2016a, b). Furthermore, earlier budbreak in seven conifers was related more to daytime than nighttime warming (Rossi and Isabel 2017), and temporal shifts in phenological phases are some of the best-known acclimation responses of plants to a changing environment. Nonetheless, how differences between nighttime and daytime warming affect tree physiology and stem growth are largely unstudied.

Changes in stem radius, as measured by automatic dendrometer, serve as a proxy for stem water status in the daily scale and stem growth over the long period (Chan et al. 2016; Deslauriers et al. 2003; Downes et al. 1999). In the short term, diurnal rhythms of changes in stem radius are linked to stem dehydration/rehydration cycles (Irvine and Grace 1997; Vesala et al. 2000; Zweifel et al. 2000; Turcotte et al. 2011), and this rhythm is divided into the distinct phases of contraction and expansion (Downes et al. 1999; Turcotte et al. 2009). During the day, transpiration decreases internal water reserves, and the water depletion accounts for 9–15% of the total daily

transpiration under unlimited water availability (Goldstein et al. 1998). During the night, water lost during the day is restored to the storage tissues, such as roots, stems, and foliage, when transpiration is minimal (Čermák et al. 2007; Goldstein et al. 1998). Furthermore, at northern latitudes, shorter nights during the summer may limit complete stem water replenishment (Kavanagh et al. 2007). Over the longer term, the replenishment of stem water reserves at night is fundamental for stem growth as irreversible xylem-cell enlargement occurs mainly at night when the hydrostatic pressure in the expanding zone reaches its highest values (Mencuccini et al. 2017; Steppe et al. 2015). So, stem expansion could be limited during the night and stem contraction could be amplified during the day. However, it is not yet clear how the pattern of even warmer nights relative to the warming days will influence the stem water balance.

Variations in stem radius are induced by changes in bark water content, which responds directly to soil and air microclimate conditions such as soil moisture availability and evaporative demand (Cocozza et al. 2012; Giovannelli et al. 2007; Mencuccini et al. 2017). Under low water availability, the loss of cell turgor in the bark and cambial region, i.e., decreased water potential, causes shrinkage of the stem. The stem will then swell as a result of tissue rehydration after rain events or irrigation (Simonneau et al. 1993). After several days of drought, the depletion of water reserves stored within the stem may represent up to 50% of the water transpired by leaves, as extreme value, although during a single day, this amount can be relatively low (Goldstein et al. 1998). Drought conditions in the boreal forest lead to multiple responses of boreal tree species. For example, Belien et al. (2014) observed that, in a mature stand of black spruce, artificial drought did not affect stem water status or radial growth during the growing season. In contrast, drought conditions in young and mixed stands of black spruce promoted stomatal closure due to a lowering of leaf water potential (Blake and Li 2003; Grossnickle and Blake 1986), as a result of the reduction in the growth (Deslauriers et al. 2014). Water reserves in the bark and elastic tissues are therefore important both to support transpiration than for buffering short- and long-term variations in cell turgor in developing tissues (i.e., developing phloem and xylem). Further research is required to elucidate the response and recovery capacity in the short term of boreal conifers to drier conditions.

Given that projections of climate change in the boreal region involve both increased temperatures and drought frequency (IPCC 2014), we expect that this combination may result in complex and unexpected interactions. High temperatures can make plants more vulnerable to drought conditions (Way and Sage 2008; Zhao et al. 2013). In black locust and Douglas fir, heat stress decreases stem growth to a similar degree as drought, but the concomitant warming+drought affects leaf biomass and basal area more than control trees and trees subject to a single stress (Ruehr et al. 2016). In pine and oak, low soil water availability decreases stem height and diameter as well as total biomass much more than weekly heat waves alone (Bauweraerts et al. 2014). Although a few studies have examined the combined effects of warmer temperatures and drought conditions on boreal species, tree response to combined stressors is not necessarily linear. As a means of obtaining greater insight into the mechanisms that underlie the nonlinear response to abiotic stressors, variations in stem diameter may serve as a proxy.

This study aimed to verify the interaction between nighttime and daytime warming and drought on the stem growth in young black spruce (*Picea mariana* (Mill) B.S.P.). We hypothesized:

1. Asynchronous warming impairs the cyclical pattern of stem contraction and expansion. Daytime warming would increase stem radial contraction through increased water loss, whereas nighttime warming would reduce stem radial expansion through reduced water replenishment of the stem storage compartments.
2. Under conditions of prolonged water deficit, the emptying of stem and bark water storage would decrease the daily amplitude of stem radius contractions and lead to an overall decrease in stem radius (negative stem cycles).
3. The combination of warming and water deficit would increase the intensity of plant water stress. A more rapid emptying of water reserves combined with a slower rehydration would exacerbate the amplitude and duration of stem contraction and expansion.

2 Material and methods

2.1 Experimental design

We conducted this experiment between May and August 2011 (DOY 121–229). We used 4-year-old black spruce [*Picea mariana* (Mill.) B.S.P.] saplings that were growing in a greenhouse at Chicoutimi, Canada (48° 25' N, 71° 04' W, 150 m a.s.l.). In summer 2010, 2000 saplings were transplanted into plastic reversed-conic pots (4.5 L each). The saplings grew in an open field until the following spring. In April 2011, we

randomly selected 1104 saplings of homogeneous size (53.01 cm ± 8.8 cm in height and 10.43 mm ± 1.79 mm in diameter at the collar), and we divided these saplings among three independent sections of the greenhouse; each section was associated with a different irrigation and thermal regime. In the control thermal regime (named control temperature (CT)), we grew the plants at temperatures that matched and varied with the temperatures outside of the greenhouse. The other two sections of the greenhouse were subjected to specific thermal regimes. Plants were grown in warmer conditions either during the day [daytime warming (DW), from 0700 to 1900 hours] or during the night [nighttime warming (NW) from 1900 to 0700 hours] at a temperature ca. 6 °C higher than CT. During the experiment, continuous heating was applied through a computerized system (software and electronic thermostat, Harnois' System, QC, Canada).

During the period of maximum stem growth, saplings are highly sensitive to dry conditions (Rossi et al. 2006). As such, we applied two irrigation regimes to the saplings: (i) control (irrigated saplings) in which soil water content was maintained at 80% of field capacity; and (ii) water deficit (non-irrigated saplings) in which irrigation was withheld for 25 days in June (DOY 158–182) for three saplings per thermal condition, during the active primary growth (Zhai et al. 2012) and according to mild and severe level of water deficit shown in previous studies (Balducci et al. 2013; Grossnickle 2000).

2.2 Data collection

We measured plant water status from mid-May to mid-August 2011 (DOY 132–222) on branches of the first whorl for 18 randomly selected saplings (three saplings × three thermal conditions × two irrigation regimes per week). These saplings were subjected to the same thermal conditions and irrigation regimes as the saplings used for measurements of stem radius. We determined predawn [Ψ_{pd}] and midday [Ψ_{md}] leaf water potential using a pressure chamber (PMS Instruments, Albany, OR, USA). We measured Ψ_{pd} on a weekly basis at predawn from 0200 to 0400 hours ($n = 16$ days) and Ψ_{md} from 1000 to 1300 hours ($n = 17$ days). The volumetric water content (VWC) of the soil was measured weekly from mid-May to mid-August (DOY 131–229; $n = 34$ days) using time-domain reflectometry (TDR Fieldscout 300). We recorded the VWC at 7 cm depth in each plastic container. We replicated the measurements at each sampling, and the data were processed according to Topp et al. (2003).

We used automatic point dendrometers to monitor variations in stem radius from spring to summer (DOY 121–226). The home-made dendrometers used on the 18 randomly selected saplings (three saplings × three thermal conditions × two irrigation regimes) had a sensing rod held against the outer surface of the bark by a constant force (Annex Fig. 7). The rod was made of stainless steel. LVDT macro-sensor

PR750 (Pennsauken, NJ, USA) had a measuring range of stem radius of ± 2.5 mm and offered a core-to-bore radial clearance of 0.25 mm with the standard supplied core. For the sensor, the thermal coefficient of sensitivity was $-0.02\%/^{\circ}\text{C}$, corresponding to $0.5 \mu\text{m}/^{\circ}\text{C}$ and the linearity error was $\pm 0.25\%$ of full range output. The PR750 sensor output $V1/Vx$ ratio was converted into a value (length of sensors, mm) using a linear calibration regression (Loggernet software, Campbell Scientific, Inc., Logan, Utah). The instrument consists of a displacement transducer anchored to a plastic holder and is fixed into the soil with four screws (Annex Fig. 7). We installed one dendrometer per sapling on the stem at 5 cm above the collar. Stem size variation was recorded every 15 min and was averaged over each hour (Deslauriers et al. 2003). Due to the thermal expansion of the frame, variations in temperature did not affect sensor measurements. During the experiment, some non-irrigated saplings were partially damaged; one sapling per each thermal condition had complete needle wilting and stem necrosis. The number of analyzed saplings was therefore reduced for these three conditions starting from DOY 207 (CT), DOY 187 (DW), and DOY 186 (NW). In these days, the predawn water potentials in non-irrigated saplings were -0.6 MPa at CT and in warmer conditions ranged between -0.7 and -1.7 MPa.

2.3 Statistical analyses

For stem variation phases, stem cycle extraction was performed using a three-step procedure composed of two SAS routines (SAS 9.3, SAS Institute, Inc., Cary, NC) (Deslauriers et al. 2011). The procedure divides the series into two distinct phases: (1) contraction, the period between the first maximum radius and the following minimum radius, and (2) recovery, the period from the minimum radius until the return to the previous maximum value or when the stem begins another contraction phase (Turcotte et al. 2009; Turcotte et al. 2011). SAS routines calculated the amount of stem radius variation and the duration of the stem cycle phases (Deslauriers et al. 2011). Stem size variation was tested across irrigation regimes and thermal treatments (fixed factors) using GLM procedure in SAS for the dendrometer values on the days of measurements. Analysis of variance (ANOVA) was used to analyze differences in the amplitude and duration of the contraction and expansion phases among the different irrigation regimes, thermal treatments, and the warming \times drought interaction. Irrigation regimes and thermal treatments were defined as fixed factors, whereas trees were the random factor. For the analysis, we used a linear MIXED model procedure in SAS (SAS 9.4, SAS Institute, Inc., Cary, NC). Daily circadian stem cycle components were previously averaged among water deficit periods (before, during, and after the water deficit). The first-order autoregressive [AR(1)] provided the suitable correlation structure (Wolfinger 1993). The selection of the

first-order autoregressive [AR(1)] structure was based on the lower Akaike information criterion (AIC). Normality and homoscedasticity were verified graphically using the residual plots of the linear models (Quinn and Keough 2002).

Volumetric water content was tested across irrigation regimes and thermal treatments (fixed factors), with trees as a random factor, using a linear MIXED model procedure in SAS (SAS 9.4, SAS Institute, Inc., Cary, NC). We ran an analysis of variance for repeated measurements (ANOVAR) for leaf water potential [(Ψ_{pd}) and (Ψ_{md})]. Irrigation regimes and thermal treatments were defined as fixed factors, DOY as a repeated factor and trees as a random factor using the linear MIXED model procedure in SAS (SAS 9.4, SAS Institute, Inc., Cary, NC). The selection of the covariance structure was based on the lower AIC. Normality and homoscedasticity were verified graphically using the residual plots of the linear models. As a result, predawn leaf water potential was transformed ($1/\Psi_w$) to satisfy these requirements. In all analyses, when effects were significant, we ran least squares means (LS-means) with Student's *t* tests for paired comparisons and Tukey-Kramer tests for comparing multiple means.

Spearman correlation assessed the relationships across warming and irrigation regimes between leaf water potentials [(Ψ_{pd}) and (Ψ_{md})] and the amplitude (mm) and duration (h) of both contraction and expansion of the stem throughout the experiment.

3 Results

3.1 Growth conditions

From May to mid-August 2011 (DOY 121–226), DW and NW were, on average, 4.5 and 5.2 $^{\circ}\text{C}$ warmer than CT (Fig. 1). In CT, daily temperature averaged 17.7 $^{\circ}\text{C}$ and varied between 14 and 22 $^{\circ}\text{C}$ during the growing season, with a maximum temperature observed in July (24.3 $^{\circ}\text{C}$). During the 25 days of imposed water deficit, the VWC of the non-irrigated saplings decreased for all thermal conditions ($P < 0.0001$, Annex Table 3) and reached values near zero (ranging from 0.68 to 4%, Fig. 2) on DOY 182. Following the drought period, VWC increased quickly, and field capacity was reached about 20 days after the resumption of irrigation (Fig. 2). Then, VWC was maintained at field capacity until the end of the experiment. We observed significant differences in the VWC among all thermal conditions ($P = 0.0002$, Annex Table 3). However, we found no significant differences in the VWC between drought and warming (Annex Table 3).

3.2 Plant water status during the experiment

Among all thermal conditions, we recorded a significant decrease in Ψ_{pd} in the non-irrigated saplings during the water

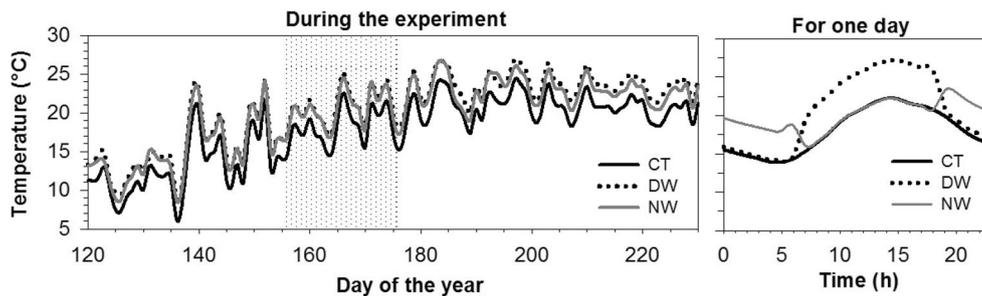


Fig. 1 (Left panel) Daily temperatures experienced by black spruce saplings in the three thermal conditions (CT, control temperature; DW, temperature increase during the day; NW, temperature increase during the night) throughout the greenhouse experiments from the end of April to the end of August (DOY 118–239). Dotted gray background corresponds to the water deficit period during June (DOY 158–182). (Right panel) Mean

temperatures over an entire day (CT, control temperature (black curve); DW, temperature increase during the day (dotted curve); NW, temperature increase during the night (gray curve)). The mean temperatures were calculated throughout the entire experiment, from May to August (DOY 121–229)

deficit period (Annex Table 4 and Fig. 8). During the water deficit period, Ψ_{pd} of the non-irrigated saplings declined significantly to -1.4 MPa in CT and -1.6 and -2.8 MPa in the DW and NW conditions, respectively (Annex Table 4 and Fig. 8). During this drought period, Ψ_{md} of the non-irrigated saplings reached -2.1 MPa, -1.95 MPa, and -2.3 MPa for CT, DW, and NW saplings, respectively (Annex Table 4 and Fig. 8), no significant differences were recorded between treatments.

3.3 Stem radius increase

The stem radius of the irrigated saplings increased progressively from May to August. Higher total stem growth values were observed under DW and NW conditions (0.92 ± 0.2 and 0.98 ± 0.1 mm, respectively) relative to CT (0.73 ± 0.2 mm) (Fig. 3). In June, we detected a plateau, a well-known phenomenon related to a stasis of primary growth (Deslauriers et al. 2016). In the non-irrigated saplings, we observed a pronounced decrease in stem radius from mid-June until the end of the water deficit (0.018 mm \pm 0.1 mm). Daily mean stem radius was 0.46 mm in irrigated saplings at the end of irrigated period (DOY 182) (Fig. 3, shaded areas). One week after rehydration (DOY 190), the pattern of increasing stem radius of the non-irrigated saplings was only partially restored (on

average 0.2 ± 0.2 mm in the non-irrigated saplings versus 0.6 ± 0.2 mm in the irrigated saplings, Fig. 3). Stem radius increased progressively until the end of the experiment. However, water deficit affected the variation in stem radius with a significant difference between irrigated and non-irrigated saplings ($P = 0.0216$, Table 1, Fig. 3).

3.4 Effect of combined stresses on the circadian stem cycle

The amplitude of stem contraction and expansion was influenced by warming and the combination of the irrigation regime \times warming (Table 2). Significant differences in stem contraction were found between CT and NW as well as between DW and NW ($P = 0.0196$, Table 2). In the non-irrigated saplings, the amplitude of stem contraction was significantly higher in CT than under both warming conditions ($P = 0.0004$, Table 2). Under the DW conditions, we observed a higher amplitude of stem expansion in the irrigated saplings compared to the non-irrigated individuals ($P = 0.0013$, Table 2). However, we found no significant differences in the amplitude of contraction and expansion between the irrigation regimes (Table 2). Further, significant differences in stem expansion were found between DW and NW ($P = 0.0335$, Table 2).

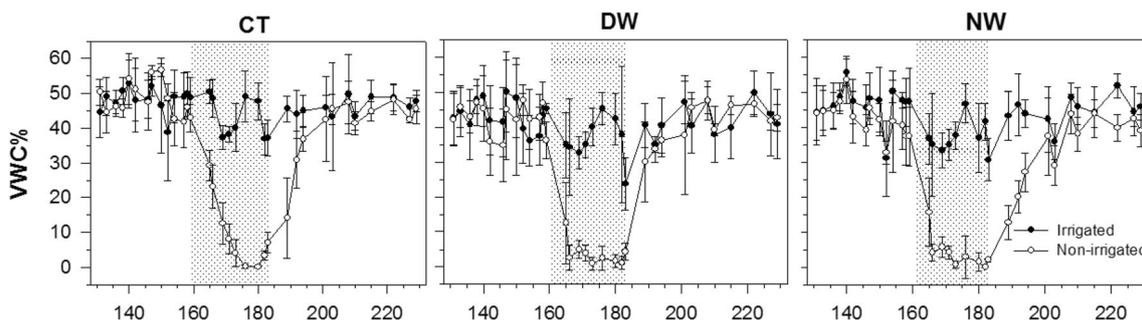


Fig. 2 Volumetric water content (VWC, %) in irrigated (black circles) and non-irrigated (white circles) saplings under three thermal conditions (CT, control temperature; DW, temperature increase during the day; NW,

temperature increase during the night). Vertical bars represent the standard deviation. Dotted gray background corresponds to the water deficit period

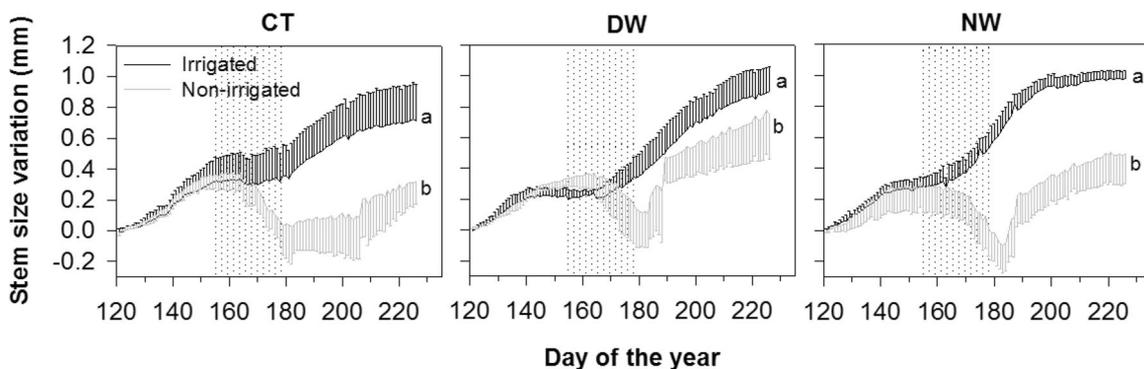


Fig. 3 Time series of stem radius increase (mm) for black spruce saplings between May and August (DOY 121–226). Black and gray curves represent irrigation regimes during the water deficit period (gray background) under the three thermal conditions (CT, control temperature; DW, temperature increase during the day; NW, temperature increase

during the night). Vertical bars represent the standard deviation. Dotted gray background corresponds to the water deficit period. Different letters above the bars denote significant differences between irrigation regimes (Student’s *t* test, for paired comparisons of means)

The highest amplitude of contraction was found in non-irrigated saplings at CT (0.18 ± 0.07 mm) when compared to DW (0.14 ± 0.05 mm) and NW (0.11 ± 0.05 mm) (Fig. 4) and after 2 weeks of water deficit imposition. For the non-irrigated saplings grown under DW and NW, lower amplitudes of expansion were observed from DOY 173 to DOY182.

Warming and irrigation regimes, as independent stressors, affected the duration of stem contraction and expansion (Table 2). However, we observed no significant differences in the duration of contraction and expansion in the combined stress irrigation regimes \times warming (Table 2). In non-irrigated saplings, the duration of contraction was significantly affected by water ($P = 0.0416$, Table 2). During the water deficit, the duration of contraction was generally greater in non-irrigated saplings when compared to irrigated ones (DOY 175, $15.3 \text{ h} \pm 7.5 \text{ h}$ versus $6.8 \text{ h} \pm 3.1 \text{ h}$) (Fig. 5). Before, during, and after the water deficit period, the duration of contraction was generally longer under DW than both CT and NW (Fig. 5). During water deficit, the highest duration of contraction lasted $24 \text{ h} \pm 9 \text{ h}$ at DW, $19 \text{ h} \pm 3 \text{ h}$ at CT, and $22 \text{ h} \pm 7 \text{ h}$ at NW (Fig. 5). The duration of expansion varied markedly due to irrigated regimes and thermal condition, ranging from 1 to 68 h (Fig. 5). During water deficit, non-irrigated saplings had a shorter duration of expansion

($6.05 \text{ h} \pm 2 \text{ h}$, DOY 182), whereas the duration was $13.1 \text{ h} \pm 4.2 \text{ h}$ for irrigated saplings (Fig. 5). Before, during, and after the water deficit period, the duration of contraction was generally longer under CT than both DW and NW (Fig. 5). During water deficit, DW ($10 \text{ h} \pm 4.4 \text{ h}$) and NW ($13.05 \pm 6.3 \text{ h}$) saplings had a shorter duration of expansion than CT saplings ($13.5 \text{ h} \pm 3 \text{ h}$) (Fig. 5).

3.5 Relationship between plant water status and stem radius variations

In non-irrigated saplings, the duration of contraction and leaf water potentials under warming showed a significant negative correlation. Specifically, the duration of contraction was significantly correlated with Ψ_{pd} under DW conditions ($\rho = -0.51$, $P = 0.0447$, Fig. 6a, Annex Fig. 9 and Table 5), whereas the duration of contraction was most correlated with Ψ_{md} under NW conditions ($\rho = -0.61$, $P = 0.013$, Fig. 6a, Annex Fig. 9 and Table 5). Under DW, the duration of expansion and Ψ_{pd} were positively

Table 1 Summary of GLM model showing the effects of irrigation regimes (Water), thermal conditions (Temperature), and crossed factors at the last day of measurements on stem radius variation in black spruce saplings during the greenhouse experiments in 2011. Significant effects ($P < 0.05$) are in italics

Source of variation	<i>df</i>	<i>F</i> value	<i>P</i>
Stem radius variation			
Water	1	7.70	<i>0.0216</i>
Temperature	2	2.27	0.1591
Water \times Temperature	2	0.70	0.5239

Table 2 Summary of mixed model results showing the effects of irrigation regimes (Water), thermal conditions (Temperature), and crossed factors on amplitude (top) and duration (bottom) of stem radius contraction and expansion in black spruce saplings in a controlled greenhouse setting. Significant results ($P < 0.05$) are in italics

Source of variation	<i>df</i>	Contraction		Expansion	
		<i>F</i> value	<i>P</i>	<i>F</i> value	<i>P</i>
Amplitude					
Water	1	0.0071	0.9367	2.0095	0.2293
Temperature	2	4.3064	<i>0.0196</i>	3.6718	<i>0.0335</i>
Water \times Temperature	2	9.4342	<i>0.0004</i>	7.7987	<i>0.0013</i>
Duration					
Water	1	8.7595	<i>0.0416</i>	23.9006	<i>0.0081</i>
Temperature	2	11.8808	<i>< 0.0001</i>	3.699	<i>0.0327</i>
Water \times Temperature	2	0.2748	0.761	1.4503	0.2455

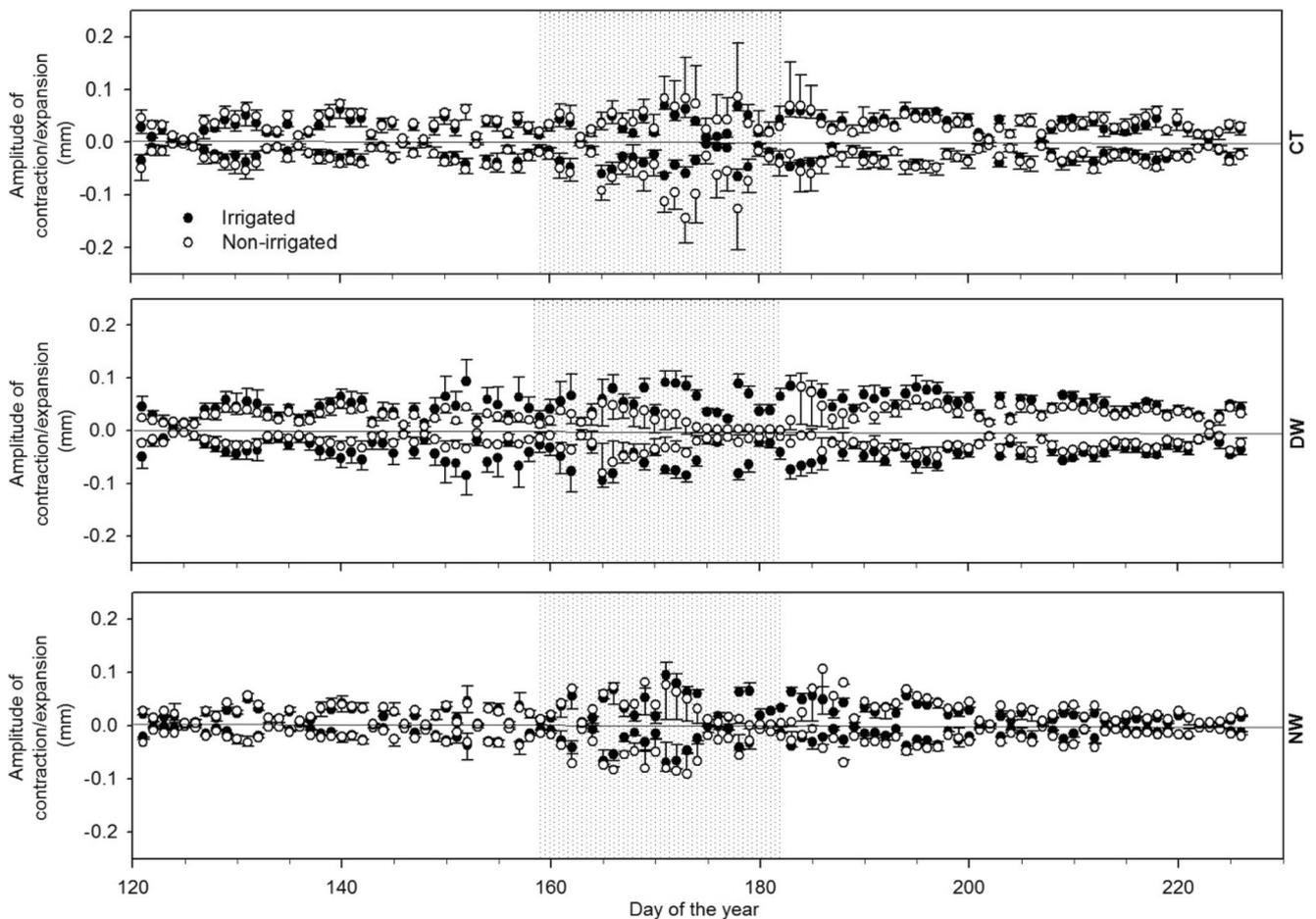


Fig. 4 Daily amplitude (mm) of the contraction and expansion phases of black spruce saplings for each thermal condition (CT, control temperature; DW, temperature increase during the day; NW, temperature increase

during the night). Black and white circles correspond to irrigation regimes. Dotted gray background corresponds to the water deficit period

correlated ($\rho = 0.67$, $P = 0.0042$) as were the duration of expansion and Ψ_{md} ($\rho = 0.57$, $P = 0.02$) (Annex Table 5). In irrigated saplings, the amplitude of expansion had a significant negative correlation with Ψ_{md} under DW ($\rho = -0.53$, $P = 0.0364$). We observed no other significant correlations for the irrigated saplings.

Under daytime warming, significant positive correlations were obtained between Ψ_{pd} and stem expansion for both amplitude ($\rho = 0.37$, $P = 0.0390$, Fig. 6b and Annex Table 5) and duration ($\rho = 0.46$, $P = 0.0077$, Fig. 6b and Annex Fig. 10) Ψ_{md} and stem shrinkage for both amplitude ($\rho = -0.37$, $P = 0.035$) and duration ($\rho = -0.50$, $P = 0.0038$, Fig. 6b, Annex Fig. 10 and Table 5).

4 Discussion

In our study, soil water availability was the major driver of plant water status and daily stem variation in black spruce saplings. The effect of asymmetric daily warming on the amplitude and duration of stem contraction and

expansion was linked to changes in the plant water potential, Ψ_{pd} and Ψ_{md} . Water deficit decreased stem growth during the growing season. The application of concurrent abiotic stresses—interaction between asynchronous warming and water deficit—affected significantly the amplitude of stem contraction and expansion, whereas both abiotic stresses did not exacerbate the duration of these phases relative to single-stress treatments.

4.1 Daytime versus nighttime warming

Daytime warming affected the duration of both stem contraction and expansion. Under nighttime warming, the amplitude of stem contraction and expansion decreased significantly, validating our first hypothesis.

Under daytime warming conditions, as compared to the control and nighttime warming, stem contraction lasted significantly longer, whereas stem expansion was significantly shorter. Under daytime warming conditions, the duration of the contraction lasted about 2 h longer than the under other conditions, resulting in a delay for

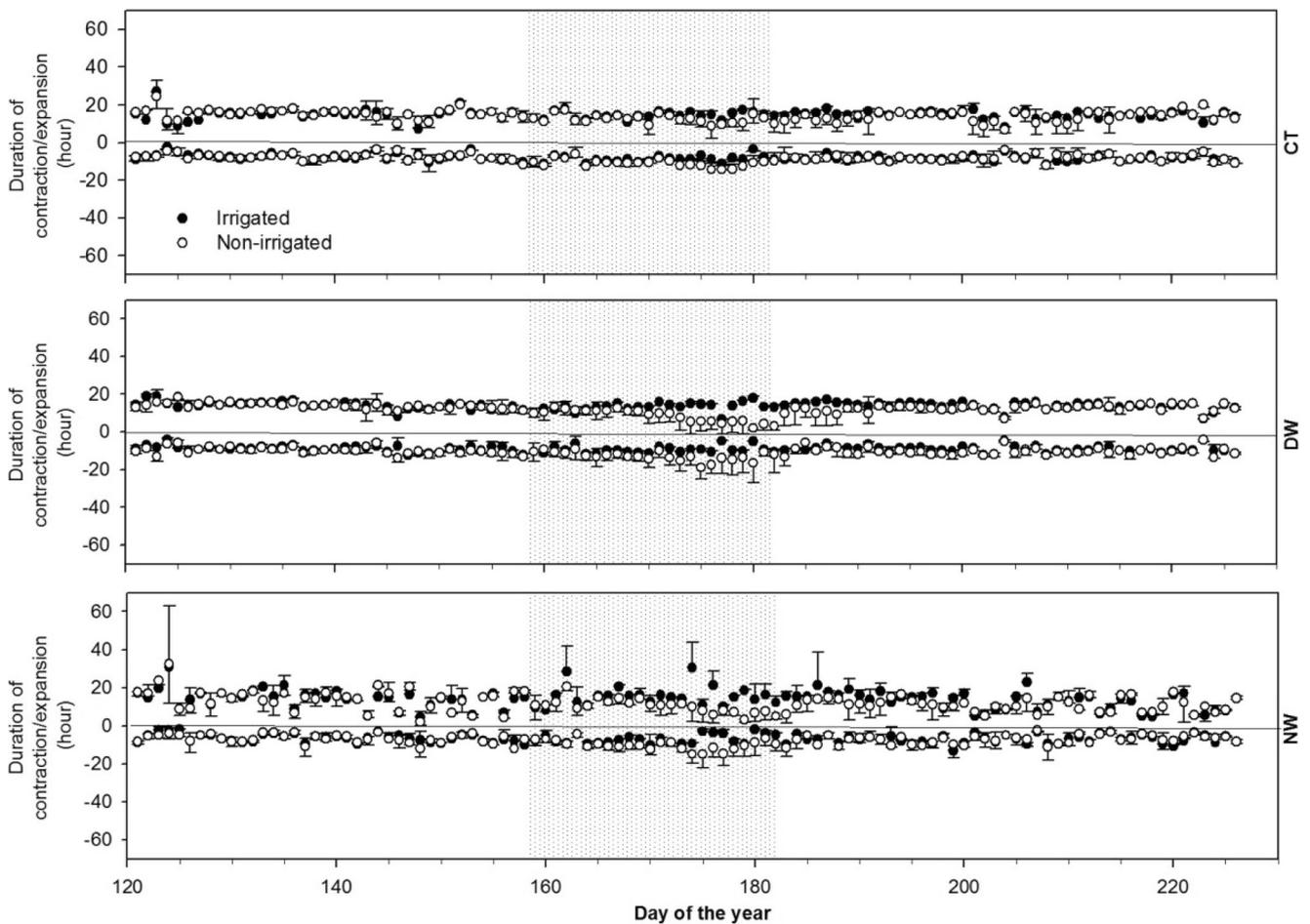


Fig. 5 Daily duration (hours) of the contraction and expansion phases for irrigated (black bars) and non-irrigated (white bars) saplings and among the three thermal conditions (CT, control temperature; DW, temperature

increase during the day; NW, temperature increase during the night). Vertical bars represent the standard deviation. Dotted gray background corresponds to the water deficit period

nighttime swelling (Drew et al. 2008; Sevanto et al. 2002). Therefore, the water refilling of the bark tissue during the night occurred faster under daytime warming. Under daytime warming, the duration of contraction and expansion were mainly regulated mainly by the predawn water potential. Stem expansion (in terms of both amplitude and duration) were correlated positively with predawn water potential (i.e., Ψ_{pd} was less negative with increasing expansion). Previous studies had demonstrated that stem growth occurred during the night when lower values of leaf water potential reduced xylem tension (Daudet et al. 2005; Hölttä et al. 2010; Steppe et al. 2006). In Scots pine, stem swelling and shrinking were associated with osmotic concentrations in the cambial and xylem regions over a 24-h period (Chan et al. 2016; Mencuccini et al. 2013), and similar results were reported for poplar (Traversari et al. 2018). In our study, a higher expansion was observed at the lowest values of Ψ_{pd} when daytime heating had not yet begun. Chan et al. (2016) observed similar patterns with modeled data where maximum change between increases in radius increment and

the osmotic gradient (stem swelling) occurred only after the lowest stem water potential was reached, between midnight and noon of the following day.

Under nighttime warming conditions, the amplitude of stem contraction and expansion decrease significantly compared to the other thermal conditions (control and daytime). Low nighttime temperature influences negatively stem increment and expansion in *Eucalyptus globulus* and *Fitzroya cupressoides* (Drew et al. 2008; Urrutia-Jalabert et al. 2015). The amplitudes and duration of contraction were mainly associated with Ψ_{md} . As a result, a shorter-lasting and a more-limited amplitude contraction phase under less negative Ψ_{md} mirrored the reduced replenishment of water storage compartments during the day and, consequently, a reduced stem expansion (faster water replenishment) during the night.

Compared to daytime warming, we detected less difference between Ψ_{pd} and Ψ_{md} under a nighttime warming regime (Annex Fig. 8). Thus, under nighttime warming conditions, saplings could maintain high turgor and cell expansion during the night. However, a low Ψ_{pd}/Ψ_{md} ratio can also be achieved

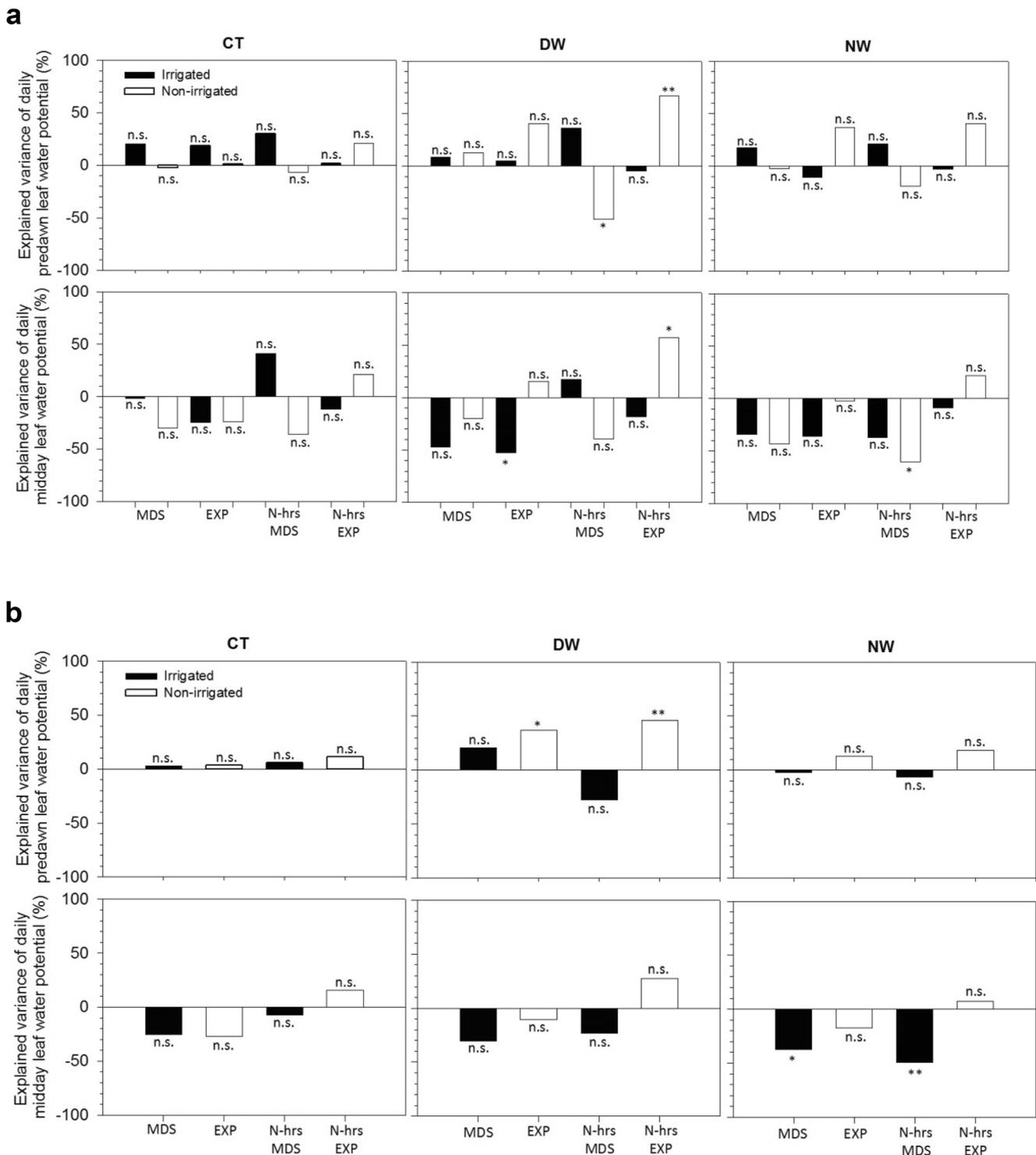


Fig. 6 Spearman correlation coefficients between leaf water potential [predawn (Ψ_{pd} , MPa) and midday (Ψ_{md} , MPa)] and amplitude (mm) and duration (h) of stem radius contraction (MDS) and expansion (EXP) in a controlled greenhouse setting. **a**) Interactions between irrigation regimes (irrigated and non-irrigated saplings) and thermal conditions (control CT; temperature increase during the day, DW; temperature

increase during the night NW); **b**) Interactions among thermal conditions are presented as control CT; temperature increase during the day, DW; and temperature increase during the night, NW. Asterisks represent significant correlations, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$, and n.s. not significant correlations. Black and white vertical bars correspond to irrigation regimes (irrigated and non-irrigated saplings)

by stomatal regulation (Bréda et al. 2006; Cochard et al. 2002) to promote circadian responses under nighttime warming.

Elevated nighttime temperatures increase photosynthesis the following day, thereby altering the net plant carbon uptake

(Turnbull et al. 2002). Furthermore, increased respiration under nighttime warming has a negative influence on leaf soluble sugars and starch concentrations by inducing a rapid turnover in carbohydrates. This, in turn, contributes positively to a growth increase (increased sink demand) (Turnbull et al. 2002). Thus, in our study, the shorter stem expansion observed under nighttime warming could explain a more conservative water use that led to a higher cell turgor leading to higher stem growth. Previous study demonstrated that the rate of growth was twice as fast under nighttime warming compared to daytime warming, promoting stem growth under optimal nighttime temperatures (Balducci et al. 2016).

4.2 The duration of swelling/shrinkage related to water deficit

As the daily amplitude of contraction and expansion did not change between irrigation regimes, our second hypothesis was rejected. However, water deficit affected the duration of both contraction and expansion and the increases in stem radius.

Other studies have reported an increase in the amplitude of stem shrinkage under water deficits, and they have used the amplitude of stem shrinkage as an indicator of the intensity of water stress (Hinckley and Bruckerhoff 1975; Li and Huguet 1990). However, our findings confirm previous observations of mature black spruce where artificial drought did not alter the amplitude of stem contraction (Belien et al. 2014). These results could be explained partly by the ability of this boreal species to regulate water loss by reducing transpiration (Meinzer et al. 2008) and to prevent dehydration during water stress by mobilizing non-structural carbohydrates (Deslauriers et al. 2014). Water reserves in the bark and elastic tissues are also important for buffering the short- and long-term variations in cell turgor.

In our study, the duration of stem contraction in the non-irrigated saplings increased significantly by about 1 h compared to the irrigated saplings and attained 9 h of stem contraction. The duration of contraction increased to about 14–15 h in correspondence with a drop of Ψ_{md} to less than -1.7 MPa under conditions of severe water deficit. Values of Ψ_{md} at -1.7 MPa may represent a threshold for limiting the duration of contraction in non-irrigated saplings. In boreal conifer seedlings, a reduction of leaf predawn water potential was observed to be the first signal of water deficit (Balducci et al. 2013; Grossnickle et al. 1991). Under mild stress, the increase of stem contraction mirrored the loss of water from stem storage compartments (bark and phloem) toward the xylem to support transpiration.

The duration of expansion in non-irrigated saplings decreased significantly by ca. 2 h compared to irrigated saplings. This duration was 5–6 h when both Ψ_{pd} and Ψ_{md} water potentials were less than -1.6 MPa. The gradient of leaf water potential between night and day is important for regulating the dynamics of water rehydration in living tissues (Turcotte et al. 2011; Zimmermann et al. 1994, 2004; Zweifel et al. 2000). In the absence of a water

deficit (well-watered conditions), average values of Ψ_{pd} and Ψ_{md} , ranging from -0.4 to -0.6 MPa, favor a longer duration of expansion in non-irrigated saplings. However, in the recovery period, this optimal water status did not induce an increase in the amplitude of expansion due to the time lag between the decrease of Ψ_{pd} and growth failure. This time lag observed in black spruce depended on the storage capacitance of the stem. This time lag has been documented at 1.44–2.5 h in herbaceous plants to 30–110 min in Scots pine (Goldstein et al. 1984; Sevanto et al. 2002). Finally, previous studies have also observed that water availability affects the circadian cycles of water depletion and replenishment in pinyon pine, especially when the duration of phases lasted more than 5–6 h (Biondi and Rossi 2015).

A significant reduction of stem radius variation between irrigation regimes mirrored the changes in the cambial region at the seasonal scale (Deslauriers et al. 2007). These results confirm that the water deficit had detrimental effects on water storage capacity and growth in the long term. These negative effects persisted even after the resumption of irrigation (Balducci et al. 2016; Rossi et al. 2012).

4.3 Combination of warming and water deficit on the daily stem cycle

The applications of concomitant stresses—warming and water deficit—produced only significant effects on the amplitude of stem contraction and expansion, whereas the duration of these phases was unaffected. Based on these results our third hypothesis was rejected.

We observed lower amplitudes of stem contraction and expansion for both irrigation regimes with no statistical difference between the other control conditions, except for the DW irrigated saplings. Under DW, the less negative Ψ_{pd} of non-irrigated saplings reduced the duration of contraction as the internal water reserves were not able to support daily transpiration. On the other hand, the decrease of Ψ_{pd} and Ψ_{md} induced a longer stem expansion of the non-irrigated saplings compared to the well-watered saplings as the increase in the duration of stem expansion mirrored longer water storage replenishment during the night. Ruehr et al. (2016) observed similar results in Douglas fir, where heat stress amplified the drought effect on plant and soil water dynamics and impaired nocturnal rehydration and diurnal transpiration and exposed plants to continuous transpiration. These relationships reflect fully the tight control of plant water potential on the diel dynamics under conditions of water stress (Steppe et al. 2015). Under nighttime warming, the mid-day water potential of non-irrigated saplings was negatively correlated with the duration of contraction (i.e., a shorter duration of contraction at less negative Ψ_{md} values). During warmer nights, similar relationships were found between predawn leaf carbohydrate status and net photosynthesis assimilation in the following day, thereby creating a greater sink demand and a lower concentration of sugars (Turnbull et al. 2002).

5 Conclusion

Drought induced an imbalance in plant water status in the short term that increased the duration of stem contraction and decreased the duration of stem expansion as well as reducing growth during the growing season. The timing and magnitude of stem circadian cycles were affected by asymmetric warming (as a single independent treatment). Under daytime warming scenarios, the duration of contraction and expansion were regulated mainly by predawn water potential, inducing longer (shorter) durations of contraction (expansion). Under nighttime warming, the smaller amplitudes of stem contraction and expansion were associated with midday water potential. However, the interaction of two abiotic stresses—night/daytime warming combined with drought—affected only the amplitude of contraction and expansion but not the duration. Our results provide evidence for an acclimation strategy of black spruce to warming and a combined warming \times drought; however, this strategy fails when the saplings are subjected to drought stress alone.

Acknowledgments We thank H. Morin, F. Gionest, G. Savard, and D. Gagnon for their support and technical advices. We give special thanks to M. Hay for checking the English text.

Funding This study was funded by the Natural Sciences and Engineering Research Council of Canada and the Consortium Ouranos.

Data availability The datasets generated and analyzed during the current study is subjected to Natural Sciences and Engineering Research Council of Canada (NSERC)'s Policy on Intellectual Property (IP). The datasets are available from the corresponding author on reasonable request with a productive partnership.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Abbreviations CT, control temperature; DW, warmer conditions during the day at a temperature ca. 6 °C higher than CT; NW, warmer conditions during the night at a temperature ca. 6 °C higher than CT; Ψ_{pd} , predawn leaf water potential (MPa); Ψ_{md} , midday leaf water potential (MPa); VWC, volumetric water content (%)

Annex

Table 3 Summary of mixed model results showing the effects of irrigation regimes (Water), thermal conditions (Temperature), and crossed factors on volumetric water content (%). Significant results ($P < 0.05$) are in italics

Source of variation	<i>df</i>	<i>F</i> value	<i>P</i>
VWC (%)			
Water	1	88.3178	< 0.0001
Temperature	2	8.8129	0.0002
Water \times Temperature	2	1.2559	0.2854

Table 4 Summary of mixed model results showing the effects of irrigation regimes (Water), thermal conditions (Temperature), day of the year (DOY), and crossed factors on predawn leaf water potential (a, Ψ_{pd} ;

MPa) and midday leaf water potential (b, Ψ_{md} ; MPa) in a controlled greenhouse setting. Significant results ($P < 0.05$) are in italics

Source of variation	<i>df</i>	Ψ_{pd} (a)		<i>df</i>	Ψ_{md} (b)	
		<i>F</i> value	<i>P</i>		<i>F</i> value	<i>P</i>
Water	1	17.94	< .0001	1	11.47	0.0008
Temperature	2	13.08	< .0001	2	0.81	0.4439
Water \times Temperature	2	3.38	0.0359	2	0.26	0.7749
DOY	15	19.5	< .0001	16	21.51	< .0001
Water \times DOY	15	5.4	< .0001	16	6.31	< .0001
Temperature \times DOY	30	2.71	0.0018	32	2.80	0.0012
Water \times Temperature \times DOY	30	2.84	0.0012	32	1.09	0.3989

Table 5 Spearman correlation coefficients between leaf water potential [predawn (Ψ_{pd} , MPa) and midday (Ψ_{md} , MPa)] and amplitude (mm) and duration (h) of stem radius contraction (MDS) and expansion (EXP) in a controlled greenhouse setting. (a) Interaction between irrigation regimes (irrigated and non-irrigated saplings and thermal conditions (control CT;

temperature increase during the day, DW; temperature increase during the night NW). (b) Interactions between thermal conditions are presented as control CT; temperature increase during the day, DW; and temperature increase during the night, NW. Asterisks represent significant correlations, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$

(a)	Irrigated			Non-irrigated		
	CT	DW	NW	CT	DW	NW
Ψ_{pd}						
MDS (mm)	0.20	0.08	0.18	-0.03	0.13	-0.03
EXP (mm)	0.18	0.05	-0.10	0.01	0.41	0.37
MDS (h)	0.30	0.37	0.21	-0.07	-0.51*	-0.19
EXP (h)	0.02	-0.05	-0.03	0.21	0.67**	0.41
Ψ_{md}						
MDS (mm)	-0.01	-0.47	-0.34	-0.30	-0.20	-0.43
EXP (mm)	-0.24	-0.53*	-0.36	-0.24	0.16	-0.02
MDS (h)	0.41	0.18	-0.37	-0.36	-0.40	-0.61*
EXP (h)	-0.12	-0.18	-0.09	0.21	0.57*	0.22
(b)						
	CT	DW	NW			
Ψ_{pd}						
MDS (mm)	0.03	0.20	-0.03			
EXP (mm)	0.03	0.37*	0.13			
MDS (h)	0.06	-0.28	-0.06			
EXP (h)	0.11	0.46**	0.18			
Ψ_{md}						
MDS (mm)	-0.26	-0.30	-0.37*			
EXP (mm)	-0.27	-0.11	-0.18			
MDS (h)	-0.07	-0.23	-0.50**			
EXP (h)	0.16	0.28	0.07			

Fig. 7 Dendrometer (shown at different angles) installed on the stem surface of a black spruce sapling during the greenhouse experiments (source photo: L. Balducci)



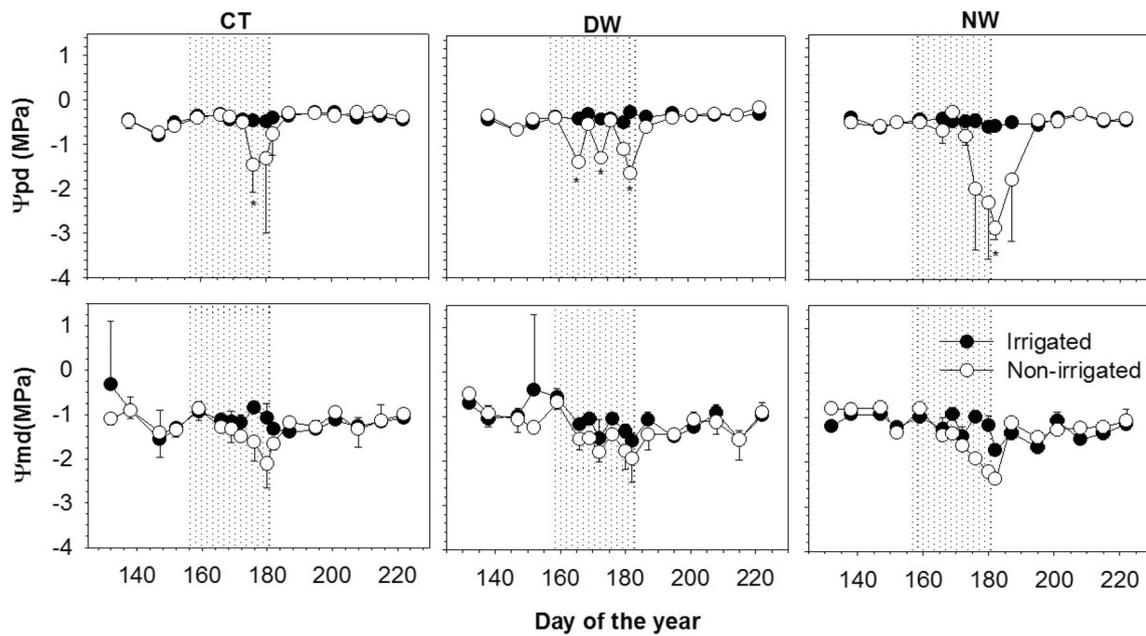


Fig. 8 Predawn leaf water potential (Ψ_{pd} ; MPa) and midday leaf water potential (Ψ_{md} ; MPa) of black spruce saplings before, during, and after the water deficit period under warming treatments (CT, control temperature; DW, temperature increase during the day; NW, temperature increase during the night). Black and white circles

correspond to irrigation regimes. Vertical bars represent the standard deviation of the average predawn and midday leaf water potentials. Dotted gray background corresponds to the water deficit period. Asterisks represent significant values for the day of the year (DOY) at $P < 0.05$

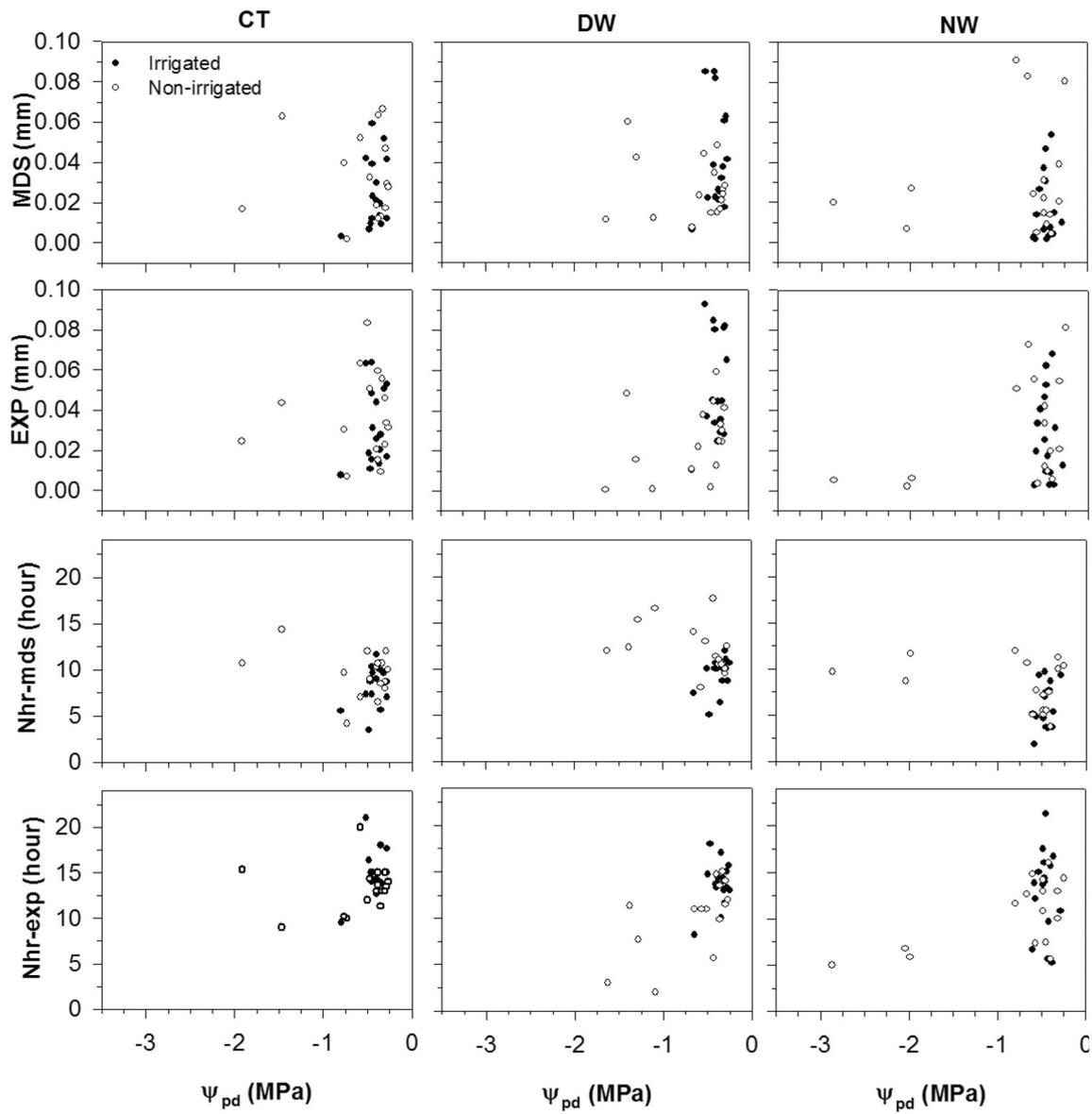


Fig. 9 Spearman correlation coefficients between predawn leaf water potential (Ψ_{pd} , MPa) and amplitude (mm) and duration (h) of stem radius contraction (MDS) and expansion (EXP) in a controlled greenhouse setting. Black and white circles correspond to irrigation regimes (irrigated and non-irrigated saplings) among thermal conditions (control CT; temperature increase during the day, DW; temperature increase during the night NW)

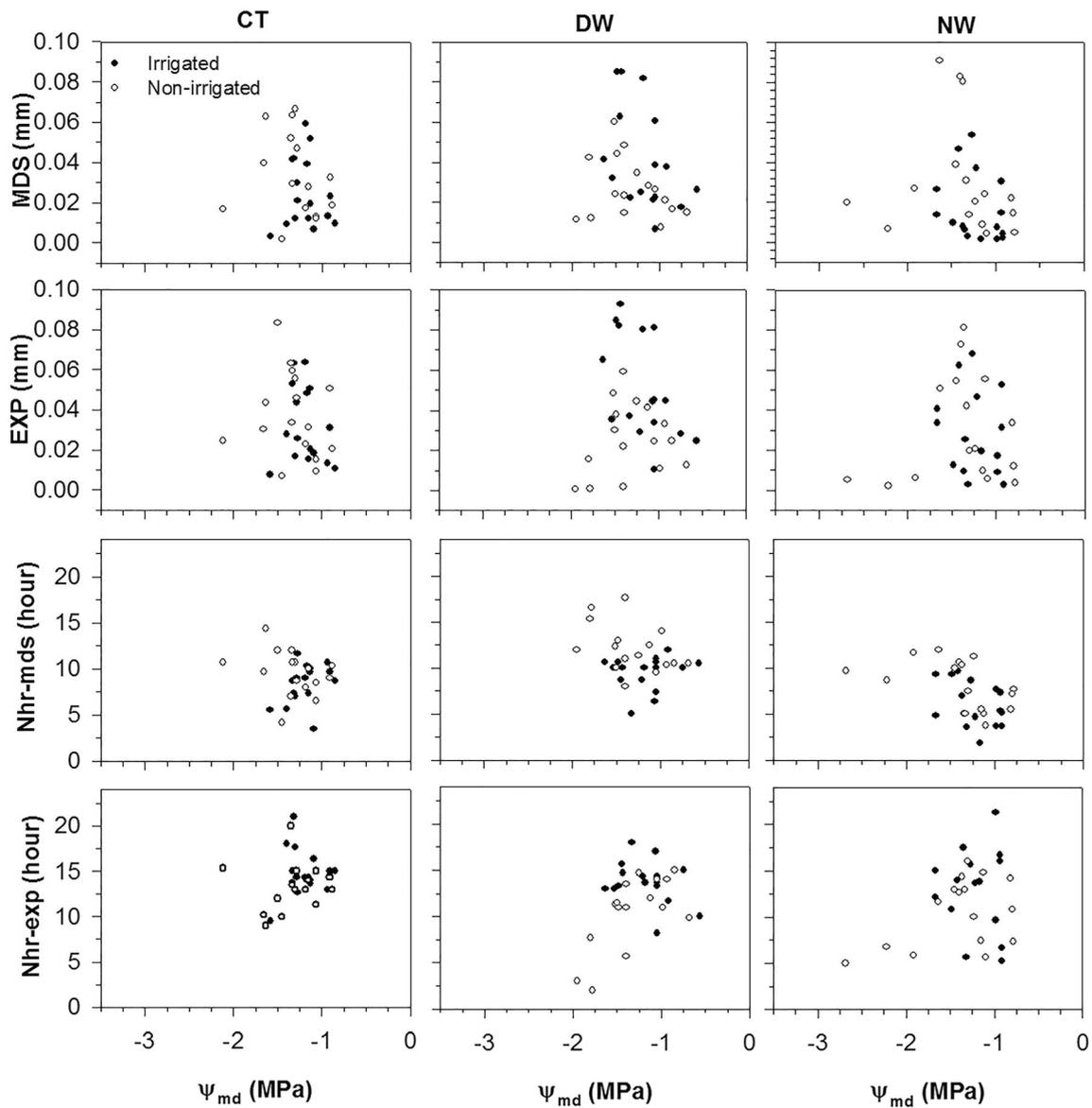


Fig. 10 Spearman correlation coefficients between midday leaf water potential (Ψ_{md} , MPa) and amplitude (mm) and duration (h) of stem radius contraction (MDS) and expansion (EXP) in a controlled greenhouse setting. Black and white circles correspond to irrigation regimes (irrigated

and non-irrigated saplings) among thermal conditions (control CT; temperature increase during the day, DW; temperature increase during the night NW)

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