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ORIGINAL PAPER

Warm temperature accelerates short photoperiod-induced growth cessation and dormancy induction in hybrid poplar (*Populus* × spp.)

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Abstract There is increasing evidence that temperature, in addition to photoperiod, may be an important factor regulating bud dormancy. The impact of temperature during growth cessation, dormancy development, and subsequent cold acclimation was examined in four hybrid poplar clones with contrasting acclimation patterns: 'Okanese'—EARLY, 'Walker'—INT1, 'Katepwa'—INT2, and 'Prairie Sky'—LATE. Four day–night temperature treatments (13.5/8.5, 18.5/13.5, 23.5/8.5, and 18.5/3.5°C) were applied during a 60-day induction period to reflect current and predicted future annual variation in autumn temperature for Saskatoon, SK. Warm night temperature (18.5/13.5°C) strongly accelerated growth cessation, dormancy development, and cold acclimation in all four clones. Day temperature had the opposite effect of night temperature. Day and night temperatures appeared to act antagonistically against each other during growth cessation and subsequent dormancy development and cold acclimation. Growth cessation, dormancy development, and cold acclimation in EARLY and LATE were less affected by induction temperature than INT1 and INT2 suggesting that genotypic variations exist in response to temperature. Separating specific phenological stages and the impact by temperature on each clone revealed the complexity of fall phenological changes and their interaction with temperature. Most importantly, future changes in temperature may affect time to growth cessation, subsequently altering the depth of dormancy and cold hardiness in hybrid poplar.

Keywords Bud dormancy · Temperature · Adaptation · Climate change

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Introduction

Temperate woody plants annually cycle through a period of active growth and a period of growth cessation and dormancy. In early autumn, the transition from active growth to the dormant phase occurs. This transition is a necessary step for winter survival of woody plants in temperate regions. Over the next 75 years, the global annual mean temperature is forecast to increase between 1.1 and 6.4°C (IPCC 2007). The impact of this temperature increase on phenological processes associated with the growth cessation, the induction of dormancy, and cold hardiness in temperate woody plants is relatively unknown. Temperature increases will be more pronounced at northern latitudes, including the Great Plains region of North America. In autumn, when dormancy levels and cold hardiness normally increase in temperate woody plants, temperatures are forecast to elevate by 3–5°C (Wheaton 2001) in the Great Plains region, thereby extending the growing season (Motha and Baier 2005). It is generally assumed that woody plants will be able to take advantage of the increase in length of growing season.

Growth, growth cessation, and dormancy (induction, maintenance, and release) are sequential and interconnected processes in the annual life cycle of plants. Growth cessation is important for winter survival of woody plants

and a prerequisite for dormancy development and cold acclimation (Weiser 1970; Fuchigami et al. 1971; Ruttink et al. 2007). Timing of hardiness development is as important as the absolute cold hardiness. These processes are of particular importance in short season, northern temperate regions, where late growth cessation and dormancy attainment would not permit full cold hardiness to be attained (Smithberg and Wesier 1968). A meta-study linked unfavorable autumn conditions and low mid-winter temperatures to winter injury in Finnish apple orchards over a 71-year period (Lindén 2001).

Plants have adapted to be in synchrony with the available growing season. A separation of growth from the environment may impact suitability of certain species or cultivars in a geographic region.

Short photoperiod is widely accepted to be the primary regulator of growth cessation and dormancy induction in deciduous woody plants (Kramer 1936; Downs and Borthwick 1956; Nitsch 1957; Weiser 1970). However, recent studies confirmed temperature may be as important as photoperiod in dormancy induction of woody plants, particularly for northern ecotypes (Howe et al. 2000; Heide 2003; Junttila et al. 2003; Tanino 2004; Svendsen et al. 2007). In some woody plants such as apple (*Malus* sp.) and pear (*Pyrus* sp.), dormancy is induced by temperature, but not short photoperiod (Heide and Prestrud 2005). There is increasing evidence that growth cessation is the result of a combined effect of night length and air temperature (Hanninen and Kramer 2007). Warmer temperatures have been shown to induce more rapid growth cessation and deep dormancy development (Fuchigami et al. 1971, 1982; Koski and Seivanen 1985 as cited by Repo et al. 2001; Junttila et al. 2003; Heide 2003; Palonen 2006). Warm autumn temperatures have been reported to delay budbreak in northern ecotypes of birch (*Betula* sp.) (Heide 2003). Evidence indicates that autumn temperatures likely affect growth cessation and dormancy development in woody plants. However, it is not entirely clear how these responses will be attenuated by the predicted temperature increase in autumn.

In this study, we show how growth cessation, dormancy development, and cold acclimation in woody plants are influenced by temperature under photoperiod conditions that induce growth cessation. The effects of day and night temperatures were separated to determine whether changes in temperatures, during either of these periods, had the same effect on growth phenology. Four hybrid poplar clones demonstrating large differences in cold acclimation patterns determined in a previous study (Silim et al. 2005; unpublished), are used in this study; *Populus* × 'Katepwa', *Populus* × 'Okanese', *Populus* × 'Prairie Sky' and *Populus* × 'Walker'. The clones are commonly grown on the Canadian Prairies, mostly as shelterbelts and have similar growth rates. 'Okanese' (EARLY) is considered to be among the most winter hardy poplar clones available for planting on the Canadian Prairies with a relatively early initiation of cold hardiness with little annual variability. Conversely, 'Prairie Sky' (LATE), is considered to be among the least winter hardy, initiating cold acclimation later in autumn when temperatures are cooler. The initiation and maintenance of hardiness in this clone appears to be very responsive to ambient air temperatures. 'Walker' (INT1) and 'Katepwa' (INT2) display intermediate cold hardiness acclimation initiation characteristics which appear to vary from year to year. We are particularly interested on how phenological changes such as growth cessation and dormancy, in clones with contrasting hardiness patterns, will be impacted by temperature increases as predicted by climate change models. The impact of late summer and early autumn temperature on growth cessation, dormancy, and cold hardiness patterns will influence the adaptability of woody plants to climate change.

Materials and methods

Plant material and growth conditions

Four hybrid poplar clones were used in this study: *P.* × 'Katepwa', *P.* × 'Okanese', *P.* × 'Prairie Sky' and *P.* × 'Walker'. The clones are interspecific hybrids from native and exotic species developed by Agriculture and Agri-Food Canada (AAFC) at Indian Head, Saskatchewan (50°N 30.705′) and Morden, Manitoba (49° 11′N). 'Walker' is a cross between *Populus deltoides* var. *occidentalis* and *Populus* × *petrowskyana*, 'Okanese' is a cross between *P.* 'Walker' × *P.* × *petrowskyana*, *P.* × 'Katepwa' is an open-pollinated progeny of *P.* × 'Walker', and *P.* × 'Prairie Sky' is a cross between *P. deltoides* × *P. nigra*. 'Walker' is the most planted hybrid poplar on the Canadian Prairies.

Hardwood cuttings were obtained from the AAFC-Shelterbelt Centre, Indian Head, Saskatchewan in February 2006. Plants were propagated in Spencer–Lemaire root trainers (Spencer–Lemaire Industries, Edmonton, AB) filled with peat moss-perlite mixture (Sunshine # 4, Sun Gro Horticulture, Bellevue, WA) and grown in a greenhouse (20 ± 5°C) under natural light supplemented with 400 W high-pressure sodium lights (18 h photoperiod, 600 μmol m^{-2} s^{-1} PPFD). The rooting media was kept moist during rooting and establishment (approximately 2 weeks). Cuttings were watered when required, usually every 1 or 2 days. Plants were fertilized with 100 ppm N in the form of 20–20–20 (N–P–K) fertilizer plus micronutrients once every week for the first 2 weeks, and twice per week after that. After 6 weeks of growth in the greenhouse (30–45 cm

in height), uniform height plants were selected and moved to experimental treatments in controlled environment chambers (Conviron PGR15, Conviron, Winnipeg, MB). The chambers were located at the phytotron facility in the College of Agriculture and Bioresources, University of Saskatchewan, Saskatoon, Saskatchewan.

Apart from the temperature treatments, growth conditions in the chambers were light intensity of approximately 300 μmol m^{-2} s^{-1} PPFD with an equal balance of incandescent and fluorescent lights, and approximately 40–60% RH. Plants were exposed to short day (SD) 12-h photoperiods, similar to the average September photoperiod in Saskatoon (52°7′N), for 30 days. After 30 days, the photoperiod was reduced to 10 h for another 30 days to account for reduction in photoperiod in autumn. The plants were watered every other day and not allowed to dry at anytime. Plants were fertilized twice a week using the same fertilizer composition and concentration given above.

Induction temperature treatments

Four day–night temperature treatments were used during the induction period (Table 1). These temperatures were selected to reflect current and predicted future annual variation in late summer or early autumn temperature for Saskatoon, Saskatchewan. The four induction temperature treatments were produced from two mean temperatures and two day/night temperature differences. This permitted us to separately examine the impact of increased night temperature, and increased day temperature. The two mean temperatures used were the 30-year mean temperature (1961–1991) (11°C) and the predicted future mean temperature (16°C) for September in Saskatoon (2080). The two day/night temperature differences were 5 and 15°C, which accounts for diurnal variations of temperature that exist during autumn.

Measurements

Height

Plant height was measured once a week from the top of the hardwood cutting to the top of the youngest leaf primordial or apical bud ($N = 8$). Days of induction treatment until growth cessation were calculated using TableCurve2D (SPSS Inc., Chicago, IL). Regression curves using the best-fit equation, $y = a + bx^3$ where y, growth increment; x, days of induction; and a, b were the best-fit constants derived from the equation and growth data. Regression curves were fit for each plant and the x-intercept point ($x = 0$) was considered to be the date of growth cessation. The rate of growth cessation (cm $week^{-1}$ $week^{-1}$) for each plant was calculated by determining the slope of the linear portion of the growth curve. Days to growth cessation and rate of growth cessation were analyzed using a two-way (main factors were clone and temperature) ANOVA using MINITAB release 14 (Minitab Inc., State College, PA).

Table 1 Induction temperature regimes used in the study

Mean temperature (°C)	Day/night temperature difference (°C)	
	5°C	15°C
11°C[a]	13.5/8.5°C	18.5/3.5°C[a]
16°C	18.5/13.5°C	23.5/8.5°C

[a] Represents the mean temperatures for Saskatoon, Saskatchewan for the month of September based on 30-year means (1961–1991) (Environment Canada 2005)

Dormancy development

Dormancy development was measured using the bud-break method modified from Rinne et al. (1998). Plants were sampled every 10 days to determine dormancy status under environmental conditions which promote bud-break. Middle stem sections, about 10 cm below the terminal bud, were taken from each plant, defoliated, and cut into smaller, two-node sections (approximately 6 cm in length). The sections were then placed into test tubes with 5 mL distilled water and placed into an E8H model controlled environment chamber (Conviron, Winnipeg, MB) (18-h photoperiod, 23°C constant temperature). Light intensity was approximately 300 μmol m^{-2} s^{-1} PPFD as previously described. Bud-break was determined as the point at which the first leaves started to emerge from the bud scales of the dormant bud. Longer times to bud-break indicate a higher level of dormancy. The depth of dormancy was calculated as the difference between the days to bud-break (DBB) at day 60 and the days to bud-break at day 0. The depth of dormancy was analyzed using a two-way ANOVA (main factors were clone and temperature), ANOVA using MINITAB release 14 (Minitab Inc., State College, PA). The rate of dormancy induction was determined from the slope of the dormancy induction curve from the equation $y = a + b/[1 + \exp(-(x - c)/d)]$, where a, minimum DBB (not dormant); b, depth of dormancy [maximum DBB(y) – minimum DBB(y)]; c, center point (x, days) of inflection; and d, a constant derived from the data.

Cold hardiness

Cold hardiness was estimated using the electrolyte leakage method described by Flint et al. (1967). In an evaluation of cold hardiness of hybrid poplar under field conditions, this method closely correlated with actual field survival. Plants were sampled every 20 days ($N = 5$) starting at the beginning of dormancy-inducing treatments (day = 0).

The top 10 cm of the stem tissue was used for hardiness testing. Stem segments were defoliated and double rinsed with distilled water and patted dry. Stem segments were cut into approximately 1 mm sections, pooled, and randomly distributed into scintillation vials. One milliliter of distilled water and a light dusting of AgI were added to the samples to ensure ice nucleation. Samples were subjected to a pre-programmed freezing cycle and samples were frozen at three predetermined temperatures to calculate the LT_{50} temperature. The cooling rate was 2°C h^{-1} and once the predetermined temperature was met, it was held constant for 30 min and samples were removed and placed at 2°C to thaw.

Once all samples were thawed, 10 mL of distilled water was added, and samples were placed on a shaker at 90 rpm for 8 h. After shaking, samples were measured for electrical conductivity (EC) using a CON 100 Series 'Oakton' Conductivity Meter (Eutech Instruments, Singapore). Once measured, samples were placed in a water bath at 80°C for 15 min to kill remaining live tissues. Once samples cooled to ambient room temperature (normally overnight), EC was measured again. Injury index (I_j) was determined for each sample temperature in each treatment using the equation for injury index outlined in Flint et al. (1967).

Using regression curves, injury index was plotted against sample freezing temperature and the point, determined by best-fit curve, at which 50% injury index occurred, was considered to be the LT_{50}. The depth of cold hardiness was determined as the difference between the cold hardiness at day 60 and the initial cold hardiness at day 0. The depth of cold hardiness was analyzed using a two-way ANOVA (main factors were temperature and clone) using MINITAB release 14 (Minitab Inc., State College, PA). Rates of cold acclimation were determined from the slope of the cold hardiness curve over the 60-day induction period.

Experimental design

Our original model was a 2 × 2×4 factorial design. There was a 2 × 2 factorial design for temperature treatments with two mean temperatures and two day–night temperature amplitudes (Table 1) and four clones;

$$Y_{ijklm} = \mu + T_i + D_j + TD_{ij} + C_k + TC_{ik} + DC_{jk} + TDC_{ijk} + R_1 + e_{ijklm,}$$

where T, mean temperature (11 or 16°C); D, diurnal temperature amplitude (5 or 15°C); C, clone ($N = 4$); and R, replication of experiment ($N = 2$); and e, error of model. After performing the ANOVA, there was no significant replication effect and the two experiments were pooled and its SSE pooled into the error. There was also a significant interaction between mean temperature and day–night temperature amplitude ($P < 0.05$) indicating that day–night temperatures, individually, were influencing the measured parameters. Because there is a significant interaction, temperature factors cannot be discussed separately. Therefore, for the ease of interpretation, we combined the 2 × 2 factorial temperature factors into four individual temperature treatments and simplified the model to a two-way factorial design;

$$Y_{ijklm} = \mu + \mathrm{Tr}_i + C_j + \mathrm{Tr}C_{ij} + e_{ijklm},$$

where random effects were Tr, temperature treatments ($N = 4$); and C, clone ($N = 4$); and e, error of the model.

Results

Growth cessation

Short day (SD) conditions resulted in growth cessation in all four clones before the termination of the study on day 60 (Fig. 1; Table 2). Days to growth cessation corresponded with visual terminal bud set (data not shown). There was a significant interaction between clone and induction temperature on the timing of growth cessation ($P < 0.05$, Table 2). Although rank in growth cessation between temperature treatments was the same for all clones, the variability was greater in some clones than others (Table 2). The differences between the earliest and latest growth cessation between induction treatments were approximately 4, 8, 23, and 29 days for LATE, EARLY, INT2, and INT1, respectively. High variation occurred among clones for rate of growth cessation in response to induction temperature. The rate of growth cessation was most affected by induction temperature in INT1 and INT2 and least affected in EARLY and LATE (Table 2). Days to growth cessation was strongly negatively correlated ($r = -0.789$, $P < 0.05$) with night temperature, while rate of growth cessation was strongly positively ($r = 0.721$, $P < 0.05$) correlated to night temperature (Table 3).

Dormancy development

Induction temperature also strongly influenced dormancy development differently in each clone (Fig. 2). The rate of dormancy development was influenced by induction temperature (Table 2). The rate was fastest under 13.5/8.5°C followed by 18.5/13.5°C and slowest in 23.5/8.5 and 18.5/3.5°C treatments (Table 2; Fig. 2). The rate of dormancy development was least affected by the induction temperature in EARLY and LATE, but most affected in INT1 and INT2 (Table 2). In addition, the point at which dormancy levels appeared to increase was different between induction

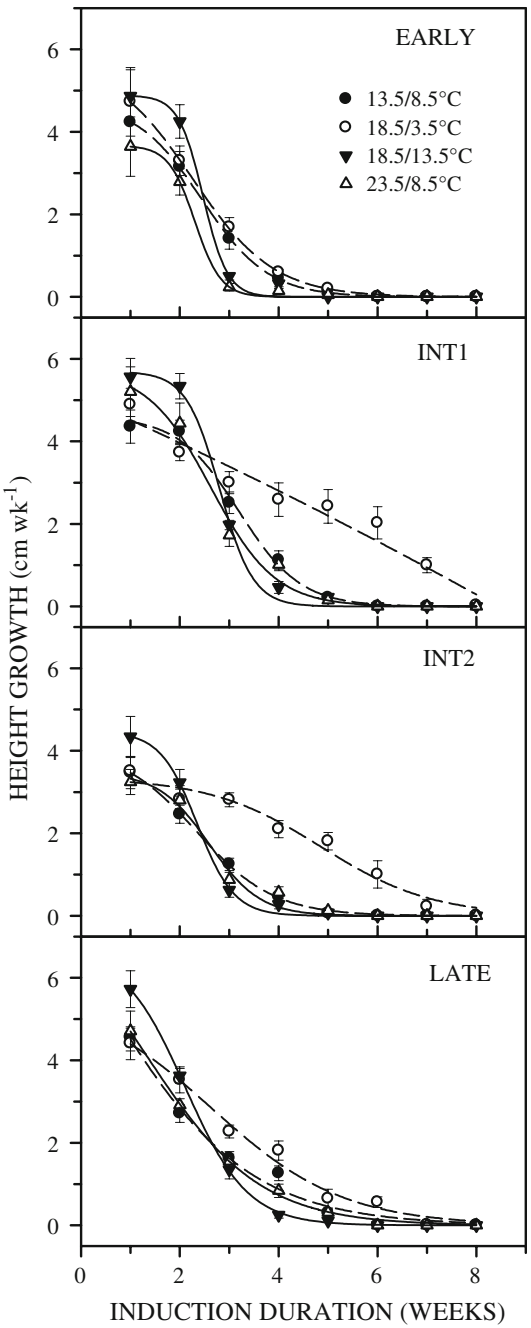

Fig. 1 Weekly growth increment (cm week^{-1}) of four poplar clones (EARLY, INT1, INT2, and LATE) under short photoperiod for four induction temperatures over a period of 60 days. *Error bars* are ±SE of the means, $N = 8$

treatments, depending on clone (Fig. 2). However, the ranking of induction treatments from earliest dormancy initiation to latest was the same for all clones with the exception of LATE in which no dormancy initiation occurred. In Fig. 2, order of dormancy initiation between induction treatments can be ordered as follows: 18.5/13.5°C < 13.5/8.5°C < 23.5/8.5°C with the exception of 18.5/3.5°C induction treatment in which dormancy induction only occurred in EARLY.

The depth of dormancy is dependent on both the timing of induction and rate of dormancy development. There was a significant interaction between induction temperature and clone for depth of dormancy ($P < 0.05$). For all clones, plants subjected to 18.5/13.5°C induction temperatures achieved the deepest level of dormancy, closely followed by those subjected to 13.5/8.5°C treatment. Conversely, plants subjected to 18.5/3.5°C achieved the shallowest level of dormancy, followed by those subjected to 23.5/8.5°C induction temperatures. Although induction temperature affected dormancy development in a similar manner for all clones, the magnitude by which temperature affected dormancy induction was different for each clone. EARLY and LATE were the least affected by induction temperature and INT1 and INT2 were most affected. The magnitude of difference in mean depth of dormancy between the extreme values (18.5/13.5 and 18.5/3.5°C induction temperatures) were approximately 3, 10, 17, and 23 days for LATE, EARLY, INT1, and INT2, respectively. However, the small difference between induction treatments was a result of dormancy development not occurring in LATE under any induction temperature (Fig. 2; Table 2). The rate of dormancy development was strongly negatively correlated ($r = -0.664$, $P < 0.05$) with day temperature. The depth of dormancy was positively correlated ($r = 0.678$, $P < 0.05$) with night temperature (Table 3). Thus, warmer day temperatures appeared to slow the rate of dormancy acquisition and warmer nights resulted in deeper dormancy.

Cold hardiness

Induction temperature affected cold acclimation differently for each clone (Fig. 3). Generally, for all clones, cold hardiness started to increase first in 18.5/13.5°C, followed by 13.5/8.5 and 23.5/8.5°C and lastly, the 18.5/3.5°C induction temperature (Fig. 3). For EARLY, there appeared to be little difference in timing of cold acclimation initiation between induction temperatures. The differences between timing of cold acclimation initiation were higher for INT1, INT2, and to a lesser extent, LATE. Plants subjected to the 18.5/13.5°C induction temperature attained a much deeper level of cold hardiness followed by those subjected to the 13.5/8.5°C induction temperature. On the other hand, smaller increases in cold hardiness were observed in plants subjected to the 18.5/3.5°C induction temperature followed by those subjected to the 23.5/8.5°C induction temperature (Table 2). Night temperature was negatively correlated with the rate of cold acclimation ($r = -0.499$, $P < 0.05$), but positively correlated with depth of cold

Table 2 Time to growth cessation, rate of growth cessation, rate of dormancy induction, depth of dormancy, rate of cold acclimation, and depth of cold hardiness for four hybrid poplar clones under four temperature regimes over a period of 60 days

Temperature regime (°C day/night)	Days to growth cessation (days)[a]	Rate of growth cessation (cm week^{-1} week $^{-1}$)[b]	Rate of dormancy induction (ΔDBB day^{-1})[b]	Depth of dormancy (ΔDBB)[a]	Rate of cold acclimation (°C day^{-1})[b]	Depth of cold hardiness (Δ°C)[a]
EARLY						
13.5/8.5°C	29.7 ab	1.03 ± 0.190	1.80 ± 0.21	28.8 a	0.47 ± 0.008	−15.9 b
18.5/3.5°C	30.6 b	0.96 ± 0.090	1.00 ± 0.17	20.2 b	0.43 ± 0.017	−13.9 c
18.5/13.5°C	27.4 ab	1.42 ± 0.135	1.20 ± 0.11	29.7 a	0.49 ± 0.026	−18.0 a
23.5/8.5°C	26.8 a	0.89 ± 0.094	1.00 ± 0.05	27.0 a	0.40 ± 0.010	−15.0 bc
INT1						
13.5/8.5°C	34.5 b	1.34 ± 0.103	2.60 ± 0.36	22.3 a	0.26 ± 0.008	−10.4 b
18.5/3.5°C	57.5 c	0.40 ± 0.070	0.30 ± 0.07	6.3 c	0.23 ± 0.008	−2.3 d
18.5/13.5°C	28.2 a	1.73 ± 0.094	2.00 ± 0.25	22.8 a	0.31 ± 0.018	−13.5 a
23.5/8.5°C	33.8 b	1.40 ± 0.144	0.32 ± 0.05	10.3 b	0.23 ± 0.006	−5.9 c
INT2						
13.5/8.5°C	33.4 b	0.82 ± 0.066	1.80 ± 0.26	27.8 b	0.40 ± 0.030	−12.9 b
18.5/3.5°C	50.9 c	0.29 ± 0.084	0.12 ± 0.07	5.3 d	0.20 ± 0.010	−3.39 d
18.5/13.5°C	29.1 a	1.05 ± 0.110	1.40 ± 0.15	32.5 a	0.40 ± 0.011	−14.79 a
23.5°C/8.5°C	29.7 a	0.89 ± 0.082	0.75 ± 0.05	12.0 c	0.14 ± 0.008	−6.59 c
LATE						
13.5/8.5°C	35.2 b	0.96 ± 0.125	0.20 ± 0.02	6.3 b	0.43 ± 0.018	−10.6 a
18.5/3.5°C	42.4 c	0.80 ± 0.068	0.15 ± 0.03	5.1 b	0.13 ± 0.010	−7.6 b
18.5/13.5°C	27.4 a	1.17 ± 0.063	0.24 ± 0.02	8.3 a	0.43 ± 0.021	−11.3 a
23.5/8.5°C	33.8 b	0.89 ± 0.034	0.16 ± 0.01	6.6 b	0.25 ± 0.008	−8.5 b

[a] Letters denote significant ($\alpha = 0.05$) differences between treatments determined using Tukey's LSD test

[b] SE of parameters determined from regression analysis in MINITAB 14

hardiness ($r = 0.615$, $P < 0.05$) (Table 3). Thus, a warmer night temperature during the induction period resulted in a faster rate of cold acclimation and a deeper level of cold hardiness. Day temperature was not significantly correlated with the depth of cold hardiness and had the inverse effect of night temperature. Cooler nights and warmer days appear to slow cold acclimation. Similar to dormancy development, the order by which temperature influenced rate of cold acclimation the most was the same for all induction treatments. However, the magnitude by which rate of cold acclimation was affected by induction temperature was different for each clone. For all clones, rate of cold acclimation was fastest in the 18.5/13.5 and 13.5/8.5°C induction treatments and slowest in the 18.5/3.5 and 23.5/8.5°C induction treatments (Table 2). Interestingly, LATE was able to acclimate despite the fact that it developed only a minimal level of bud dormancy. 18.5/3.5°C induction treatment slowed cold acclimation in INT1 and INT2 while maximum cold hardiness for all clones was observed under the 18.5/13.5°C induction treatment. Cold hardiness was greater in both INT1 and INT2 (Fig. 2) in the 13.5/8.5°C induction treatment compared with the 23.5/8.5°C treatment.

Table 3 Pearson correlation coefficients between night and day temperature and growth cessation, dormancy development and cold hardiness in hybrid poplar clones

Measured variables	Night temperature (r value)	Day temperature (r value)
Growth		
Days to growth cessation	−0.789*	−0.188 n.s.
Rate of growth cessation	0.721*	0.099 n.s.
Dormancy		
Rate of dormancy development	0.447 n.s.	−0.664*
Depth of dormancy	0.678*	−0.368 n.s.
Cold hardiness		
Rate of cold acclimation	−0.499*	−0.449 n.s.
Depth of cold hardiness	0.615*	0.303 n.s.

* $P < 0.05$, *n.s.* not significant

Discussion

In this study, we were interested in how phenological processes occurring in woody plants during autumn will be impacted by temperature changes predicted by climate

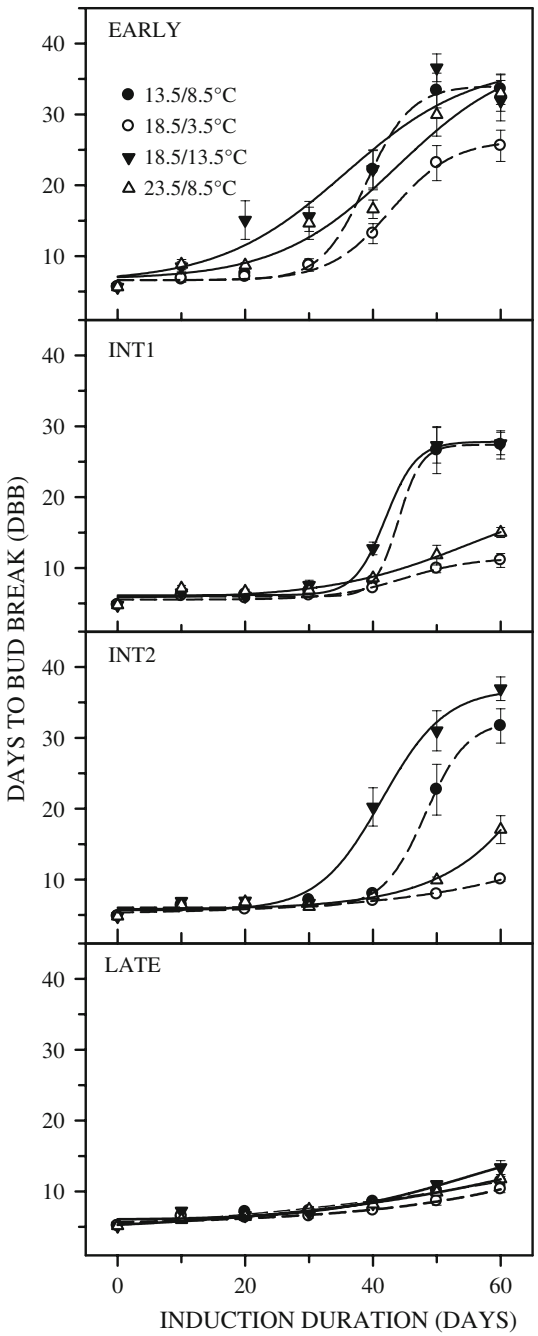

Fig. 2 Dormancy development of poplar clones (EARLY, INT1, INT2, and LATE) clones under short photoperiod for four induction temperatures over a period of 60 days. *Error bars* are ±SE of the means, $N = 16$

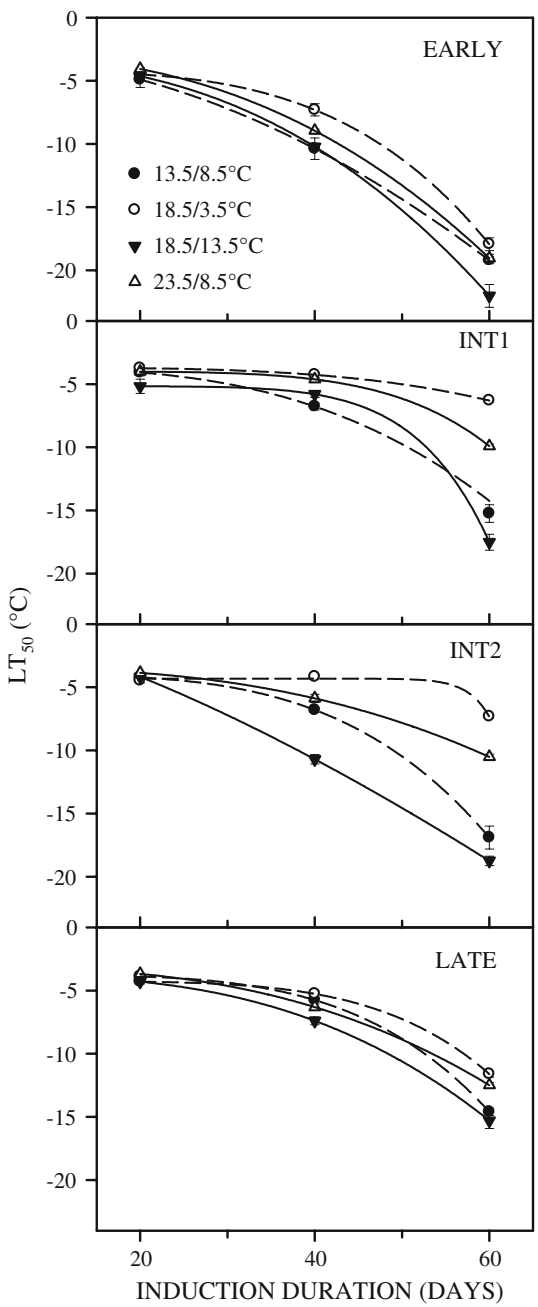

Fig. 3 Cold hardiness development of poplar clones (EARLY, INT1, INT2, and LATE) under short photoperiods for four induction temperatures. *Error bars* are ±SE of the means, $N = 8$

change models. The reference temperatures, we used for our induction treatments were based on the historical environmental data at the time when dormancy typically develops in woody plants in central Saskatchewan. We then used the predicted temperature increase expected in autumn for this region for the year 2080 (Wheaton 2001) to determine the other temperature treatments. These treatment parameters limited the extent to which we could explore the effect of extreme temperature treatments on dormancy-related processes. The results from this controlled environment study demonstrated that under short photoperiod conditions ambient temperature significantly influenced growth cessation and dormancy development.

Generally, warmer temperature treatments accelerated phenological changes in all four poplar clones. There appeared to be a difference, however, between the effects

of day and night temperatures on these processes. Overall, warmer night temperatures correlated with less time to growth cessation, greater dormancy development, and greater cold acclimation in poplar clones. Warmer day temperatures appeared to have a lesser, opposite effect. The magnitude in which temperature affected phenological processes was different between clones. Growth cessation and cold acclimation were much less affected by changes in temperatures in EARLY, and to a lesser extent LATE, than in INT1 and INT2. Other studies are in agreement with our findings and have reported that temperature can influence phenological processes in woody plants (Weiser 1970; Fuchigami et al. 1971; Heide 2003; Junttila et al. 2003; Heide and Prestrud 2005; Palonen 2006; Hanninen and Kramer 2007).

Our study identified genotypic differences in response to temperature during dormancy induction. Although our study demonstrated that cooler nights slow growth cessation in woody plants, other evidence appears to indicate that in populations or ecotypes from northern latitudes, cool temperatures can result in accelerated phenological development (Junttila 1980; Howe et al. 2000; Welling et al. 2002; Heide and Prestrud 2005; Svendsen et al. 2007). A possibility for these discrepancies from previous studies is that there is likely genetic variability in optimum temperatures for growth cessation or dormancy development (Junttila et al. 2003). In species or populations from northern latitudes where critical photoperiods for growth cessation are long and late summer temperatures are cooler, the temperature threshold for growth cessation and dormancy induction is likely lower than in species or populations from southern latitudes with shorter critical photoperiods and warmer temperatures. It is possible that cool night temperatures below an adapted temperature threshold may promote chilling that would also counteract dormancy-inducing effects during the day. However, in all cases, we believe that a temperature increase above an adapted threshold temperature, particularly during the night, would result in an accelerated growth cessation and dormancy development. Changes in temperature during exposure to short photoperiods may affect the timing of terminal bud set and dormancy development and could subsequently affect depth of dormancy.

Our study demonstrates that the clone LATE did not attain dormancy although growth cessation and cold hardiness did occur. Nevertheless, growth cessation in LATE was accelerated by warm night temperatures, but not to the extent of INT1 or INT2. The inability of LATE to attain dormancy is likely a reflection of its phenology and not the experimental treatment because observed patterns of cold acclimation of this clone in nature during autumn (Silim et al. 2005, unpublished) is similar to that of species that do not acquire true dormancy such as *Thuja plicata*, *T. occidentalis*, and *Chameacyparis nootkatensis* (Colombo and Raitanen 1991; Silim and Lavender 1994). Woody plants that maintain a deeper dormancy (higher chilling requirement) may be less susceptible to mid-winter warming (Heide 2003). Therefore, woody plants such as INT1 and INT2 under certain fall temperatures and LATE may be susceptible to winter damage in colder climates where de-acclimation can occur during mid- to late-winter warm periods. Although LATE can be susceptible to winter damage, it can survive multiple winters with little damage. The contribution of plant stress to phenological changes during autumn in woody plants was not incorporated into this experiment. Long-term field experiments may give better indications of the effect of temperature on phenological changes in woody plants in nature and may better explain survival of non-dormant clones such as LATE.

In conclusion, this controlled experiment established that temperature significantly impacts woody plant phenology during growth cessation and dormancy induction. Utilizing hybrid poplar clones enabled us to identify the effect of temperature across a range of genotypes adapted to survive in one location. However, it is difficult to generalize how woody plants will respond to temperature. Nevertheless, we cannot discount these trends. The clone LATE is an anomaly, but may be useful in future studies because LATE was unable to enter a dormant state. In the future, it may be beneficial to determine ecotypic variation in response to temperature in different populations or species of woody plants. It may be possible that the variation observed in hybrid poplar exists in natural populations of poplar in addition to other woody plant species. Warmer temperature treatments, particularly during the night, accelerated growth cessation, dormancy development, and subsequent cold acclimation in hybrid poplar.

This study has also shown that with the correct temperature combination, it may be possible to separate phenological processes, normally difficult to separate in nature, and be able to examine the molecular and physiological basis of growth cessation, dormancy and cold hardiness separately. The counteracting effects of a warmer day on some aspects of these phenological processes need to be further examined. Furthermore, warmer temperatures during the autumn could result in deeper dormancy in the plant, possibly resulting in an increased chilling requirement in some species. Lastly, these observations have implications for the understanding of impacts of temperature change during autumn on woody plant phenology and subsequent adaptation to climate change. However, the interactions between day and night temperature and contrasting diurnal effects of temperature emphasize the dynamic and complex nature of dormancy induction in woody plants.

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