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Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction

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Abstract The role of temperature during dormancy development is being reconsidered as more research emerges demonstrating that temperature can significantly influence growth cessation and dormancy development in woody plants. However, there are seemingly contradictory responses to warm and low temperature in the literature. This research/review paper aims to address this contradiction. The impact of temperature was examined in four poplar clones and two dogwood ecotypes with contrasting dormancy induction patterns. Under short day (SD) conditions, warm night temperature (WT) strongly accelerated timing of growth cessation leading to greater dormancy development and cold hardiness in poplar hybrids. In contrast, under long day (LD) conditions, low night temperature (LT) can completely bypass the short photoperiod requirement in northern but not southern dogwood ecotypes. These findings are in fact consistent with the literature in which both coniferous and deciduous woody plant species' growth cessation, bud set or dormancy induction are accelerated by temperature. The contradictions are addressed when photoperiod and ecotypes are taken into account in which the combination of either SD/WT (northern and southern ecotypes) or LD/LT (northern ecotypes only) are separated. Photoperiod insensitive types are driven to growth cessation by LT. Also consistent is the importance of night temperature in regulating these warm and cool temperature responses. However, the physiological basis for these temperature effects remain unclear. Changes in water content, binding and mobility are factors known to be associated with dormancy induction in woody plants. These were measured using non-destructive magnetic resonance micro-imaging (MRMI) in specific regions within lateral buds of poplar under SD/WT dormancing inducing conditions. Under SD/WT, dormancy was associated with restrictions in inter- or intracellular water movement between plant cells that reduces water mobility during dormancy development. Northern ecotypes of dogwood may be more tolerant to photoinhibition under the dormancy inducing LD/LT conditions compared to southern ecotypes. In this paper, we propose the existence of two separate, but temporally connected processes that contribute to dormancy development in some deciduous woody plant: one driven by photoperiod and influenced by moderate temperatures; the other driven by abiotic stresses, such as low temperature in combination with long photoperiods. The molecular changes corresponding to these two related but distinct responses to temperature during dormancy development in woody plants remains an investigative challenge.

Keywords *Cornus sericea* · Dormancy · Magnetic resonance imaging · Photoinhibition · *Populus* · Temperature

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Lack of plant environmental synchrony is considered to be the primary cause of abiotic stress injury. Plant synchrony

requires timely responses to environmental cues to minimize risk from abiotic stresses. The timing of growth cessation and dormancy, and subsequent cold acclimation, deacclimation and the depth of cold hardiness are all critical components of winter survival in temperate climates. The degree to which temperature mediates this response is important in order to determine the impact of future temperature change on timing of growth cessation and cold acclimation in woody plants.

Survival and adaptation is intricately connected with the cycle of plant growth (Sarvas 1972, 1974 cited in Hänninen and Kramer 2007). Growth cessation (GC), bud set (BS), dormancy (D; induction, maintenance and release) and cold hardiness are sequential and interconnected processes in the annual cycle of plants (Dormling 1989; Heide 2003; Junttila et al. 2003; Horvath et al. 2003; Hänninen and Kramer 2007; Kalcsits et al. 2009a). Cold acclimation appears to be dependent upon growth cessation (Weiser 1970; Fuchigami et al. 1971; Ruttink et al. 2007; Kalcsits et al. 2009a) rather than with dormancy induction. Dormancy may be more important in the maintenance and release of cold hardiness than the initiation of this process (Tanino et al. 1989). However, in short season, northern temperate regions where late growth cessation and dormancy attainment precludes full low temperature tolerance, timing of all of these responses is important to survival (Smithberg and Weiser 1968).

In northern temperate regions, the stimulus for induction of growth cessation and dormancy has, for over 85 years, been considered to be primarily controlled by short photoperiod (Garner and Allard 1923; Kramer 1936; Downs and Borthwick 1956; Nitsch 1957; Weiser 1970; Allona et al. 2008). Increasingly, we (Svendsen et al. 2007; Kalcsits et al. 2009a, b, c), and others (see Table 1 for a summary) and have shown temperature may replace or strongly mediate this short photoperiod dormancy response in woody species. Low temperature also induces GC and D in photoperiod insensitive types (Heide and Pestrud 2005) and in the herbaceous perennial weed species, leafy spurge (*Euphorbia esula*; Horvath et al. 2009a, b). Furthermore, a joint night length and heat sum model was developed which was better able to reflect growth of *Pinus sylvestris, Picea abies* and *Betula pendula* than photoperiod alone (Koski and Sievänen 1985).

However, there are seemingly contradictory growth cessation and dormancy responses to warm and cool temperature conditions in woody plants. The observed temperature responses are complicated by: (a) the differential reaction between northern and southern ecotypes, (b) temperature interaction with photoperiod, and (c) varied growth measurements (e.g., growth cessation and/or bud set and/or dormancy; in this paper, endodormancy will be referred to as "dormancy" except where specified). Also, growth cessation and bud set may not necessarily mean the bud has attained true endodormancy. Nevertheless, in reviewing the literature (Table 1), consistent temperature responses emerge across coniferous and deciduous woody plant species: (1) northern, but not southern, ecotypes will cease growth, set bud and/or enter dormancy under the combination of long day and low temperature conditions; (2) in combination with short days, warm temperatures will accelerate GC, BS or D and increase depth of dormancy in all photoperiodically-sensitive ecotypes; (3) night temperatures have a greater impact on GC, BS and D than day temperatures. Went (1948, 1953) first coined the term thermoperiodism to indicate the importance of the relation between day and night temperature. While fewer studies have examined day versus night temperatures, all have reported either warm or cool night, but not day temperatures, to more significantly impact GC or BS or D in *Pinus taeda* (Kramer 1957), *Picea sitchensis* (Malcolm and Pymar 1975), *Betula papyrifera* (Downs and Bevington 1981), *Populus tremula* × *P. tremuloides, PHYA22* (Mölmann et al. 2005), *Cornus sericea* ecotypes and its F2 population (Svendsen et al. 2007), *Populus* hybrids (Kalcsits et al. 2009a). The influence of day and night temperature was further categorized in terms of rate of growth cessation, dormancy induction, cold acclimation, depth of dormancy and cold hardiness (Kalcsits et al. 2009a). In that study, day temperature only influenced rate of dormancy development while night temperature impacted most other parameters including depth of dormancy. Håbørg (1972) showed a strong photoperiod × temperature (both day and night) × population (latitudinal, altitudinal) interaction. Day temperature was more important for leaf number and radial growth while night temperature was more important for internode length and terminal dormancy. The key criterion was the temperature in relation to the critical daylength. This has significant implications for ability of species to move northward into longer photoperiods under climate change.

Heide and Pestrud (2005) showed apple and pear cultivar GC was not sensitive to photoperiod but GC was induced by cool temperatures. Recently, Heide (2008) showed the photoperiodic response of *Prunus* is highly temperature-sensitive. Growth cessation is driven by a combined effect of night length and air temperature (Hänninen and Kramer 2007). Temperature, during the autumn period in which growth cessation and dormancy development occurs, is emerging as a critical regulating factor within the annual cycle in trees.

When combined with short photoperiods, warm temperatures have been consistently and widely shown to induce earlier GC and/or a greater depth of dormancy development across coniferous and deciduous woody species (Van der Veen 1951; Dormling et al. 1968, 1989;

Table 1 Temperature-mediated growth cessation/bud set/early dormancy induction in woody plants

Reference	Species	Source	Treatments		Response measures Growth Cessation (GC–height), Bud Set (BS—terminal bud), Endodormancy (D, evaluated through bud break)	Temperature response
			Photoperiod (h)	Temperature day/night (°C)		
Dormling et al. (1968)	*Picea abies*	Provenances: Laitamaa (66°50′N); Westerhof (51°47′N);	8, 16, 24	Constant 20 10	GC BS	Southern ecotype: cool temperature (10°C) and long days (16 h) induced GC and BS but at a later date than under 8 h and either temperature treatment. In a separate expt., the southern ecotype expressed a deeper dormancy under short days (16 h) and warmer (25°C) than cooler (20°C) induction temperatures. Northern ecotype: cool temperature (10°C) and long days (24 h) induced GC and BS at the same date as the short day (16 h) and either temperature treatment. Cool temperature treatments under long or short days induced a deeper dormancy compared to warm temperature and a short day in this northern ecotype. However, cool temperatures during dormancy induction reduced subsequent growth after bud break and either cool or warm night temperatures also induced the same response. Note: Photoperiod during bud break was influenced by the photoperiod of bud maturation—buds that matured under a short photoperiod (16 h) could break under that photoperiod whereas buds matured under 24 h could only break under 24 h
Dormling (1989)	*Pinus sylvestris*	60°41′N (W4107)	First grown under 20, 18 h and 25/15°C. Then exposed to 11, 8 h	25/15 25/5	D	Initial photoperiod of plant production influenced subsequent dormancy under experimental photoperiod treatments. In the absence of chilling requirement, shorter photoperiod (18 h) significantly reduced D in both 25/15 and 25/5°C treatments compared to the 20 h photoperiod during plant propagation
		57°25′N (H1019)	First grown under 16 h, 25/15°C, then photoperiod reduced over the next 8 weeks to 8 h	25/15 25/5	GC	The 8 h and 25/15°C conditions reduced growth cessation to about 50 mm compared to 150 mm under the 25/5°C treatment
Downs and Bevington (1981)	*Betula papyrifera*	16 Latitudinal ecotypes between 67°09′N and 38°39′N	9 h Photoperiod with a 3 h night interruption to produce a long day effect	18/14, 22/14, 26/14, 30/14 30/14, 30/18, 30/22, 30/26	BS	Under long day conditions, day temperature had no influence on bud set in southern ecotypes but in northern ecotypes, BS linearly increased with deceasing day temperature (18/14 induced 100% BS). Under long day conditions, cool night temperature induced 100% BS in all northern ecotypes but BS was reduced at the highest 30/26°C treatment. In southern ecotypes, only the cool night 30/14°C treatment induced 100% BS, and BS steadily declined to 0% under the high night 30/26°C treatment

Table 1 continued

Reference	Species	Source	Treatments		Response measures Growth Cessation (GC–height), Bud Set (BS—terminal bud), Endodormancy (D, evaluated through bud break)	Temperature response
			Photoperiod (h)	Temperature day/night (°C)		
Fuchigami et al. (1971)	*Cornus stolonifera* (renamed *C. sericea*)	Minnesota, North Dakota	10–12	20/15 15/5	GC	Cool temperature treatment advanced growth cessation under short day conditions in the two northern races. However, SD/WT pre-treatment increased cold hardiness over SD/LT conditions under subsequent cold acclimation
Granhus et al. (2009)	*Picea abies*	66°25′N 60°35′N 58°35′N	12	Constant 12 21	D	Greater depth of dormancy in all ecotypes with the 21°C induction temperature compared to the 12°C treatment
Håbørg (1972)	*Betula pubescens*	70°20′N—50 m ASL 63°20′N—50 m 56°20′N—50 m 61°30′N—1000 m 61°30′N—600 m 61°30′N—200 m	12, 14, 16, 18, 20, 24	8/8, 8/13, 8/18 13/8, 13/13, 13/18 18/8, 18/13, 18/18	GC	Photoperiod × temperature × population interactions for both day temperature and night temperature on growth. Day temperature was more important for leaf number and radial growth while night temp. was more important for internode length and terminal dormancy. Low night temperature (8°C) extended the time to GC in all populations around the critical daylength—but GC for the northernmost (70°20′N, 63°20′N) and the ecotype at the highest altitude (1000 m) was less sensitive to night temperature than the other 3 ecotypes. However, under 24 h daylength, low night temperature caused earlier GC and terminal dormancy. Key was the critical daylength—and the temperatures in relation to this parameter
Heide (1974)	*Picea abies*	5 Ecotypes from 64°N (L1) 61°30′N (A2) 58°30′N (F1) 47°10′N (Gas 15) 47°04′N (Lankowitz)	14, 16, 18, 20, 24	Constant 12 15 18 21 24	GC BS	In all ecotypes, warm temperatures and short days accelerated GC and cool temperature delayed this response, particularly near the critical photoperiod. Also, long day and cool temperature conditions induced GC in all ecotypes with the northern-most ecotypes (L1, A2, F1) being the most responsive
Heide (2003)	*Betula pendula*, *B. pubescens*, *Alnus glutinosa*	60–61°N in Norway	10	Constant 9 15 21	D	In all ecotypes, warmer temperatures induced a greater depth of dormancy (greater chilling requirement needed to break bud)

Table 1 continued

Reference	Species	Source	Treatments		Response measures Growth Cessation (GC–height), Bud Set (BS—terminal bud), Endodormancy (D, evaluated through bud break)	Temperature response
			Photoperiod (h)	Temperature day/night (°C)		
Heide and Pestrud (2005)	*Malus pumila* 'A2'	Sweden	10, 24	Constant 9	GC	Apple and pear cultivars GC were not sensitive to photoperiod but GC was induced by cool temperatures. Endodormancy induction was confirmed
	M. pumila 'B9'	Russia		12		
	M. pumila 'M9'	UK		15		
	M. pumila 'MM106'	UK		21		
	Pyrus communis 'Brokmal'	USA				
Heide (2008)	*Prunus avium*	Vestby, Norway	10, 24	Constant 9	GC	Pronounced photoperiod × temperature interaction. At higher temperatures (21°C), active growth was photoperiod independent. At mid temperatures (15°C and 12°C), growth became more photoperiodically-sensitive. At 9°C, only 'Gisela 5' sweet cherry also required short days to cease growth, all other crops ceased growth under long days and low temperature conditions
	P. cerasus 'Gisela 5'	Giessen, Germany		12		
				15		
	P. cerasus 'Weiroot'	Weihenstephan, Germany		21		
	P. insititia 'St. Julien A'	East Malling, UK				
	P. insititia 'Weito'	Weihenstephan, Germany				
Howe et al. (2000)	*Populus hybrids*	*P. trichocarpa* × *P. deltoides* progeny	Field conditions (St. Paul, MN 44°59′) and greenhouse (8 h)	Average of 30.3/19.7°C under greenhouse conditions	BS	Since the natural photoperiod in a warm greenhouse was ineffective in promoting bud set compared to the field, it was concluded that other factors and most likely temperature, were responsible for bud set induction
Jonkers (1979)	*Malus domestica* 'Golden Delicious' on M. 9 rootstock. Three year old plants		16	Constant 9	D	Warmer temperatures induced deeper dormancy
				12		
				15		
				18		
				21		
				24		

Table 1 continued

Reference	Species	Source	Treatments		Response measures Growth Cessation (GC–height), Bud Set (BS—terminal bud), Endodormancy (D, evaluated through bud break)	Temperature response
			Photoperiod (h)	Temperature day/night (°C)		
Junttila (1980)	*Salix pentandra*	Two ecotypes of each species at: 69°37′N and 59°40′N	12, 14, 16, 18, 20, 22, 24	Constant 9 15 21	GC	Photoperiod × temperature interaction. GC was induced earlier under fluctuating lower night temperatures than constant temperatures particularly in the northern ecotypes under long photoperiods. *Salix* was more sensitive than *Betula* for this response
	Betula pubescens		12, 15, 18, 21, 24	15 15/9 15/6		
Junttila (1982)	*Salix pentandra*	Ecotypes at: 69°37′N, 64°28′N 59°40′N and their crosses	24	21/9 18/9	GC BS	Fluctuating temperatures induced GC in the northern but not the southern ecotype. Southern ecotypes were more sensitive to light intensity than northern ecotypes. Progenies were more similar in GC response to the southern ecotype than the northern ecotype
Junttila et al. (2003)	*Betula pubescens* *Betula pendula*	6 Ecotypes of *B. pubescens* (from 59°47′N to 70°39′N) 2 ecotypes of *B. pendula* at 59°35′N and 67°03′N	12	Constant 9 12 15 18 21	GC D	In both species, dormancy advanced most rapidly under the 12, 15 and 18°C treatments. It was delayed under 9 and 21°C. Chilling requirement increased with increasing temperature
Kalcsits et al. (2009a)	*Populus* × spp. (hybrids)	'Okanese' (Early cold acclimator) 'Walker' and 'Katepwa' (Intermediate) 'Prairie Sky' (Late) All clones are interspecific hybrids of trees adapted to 50°30′N and 49°11′N	12–10	23.5/8.5 13.5/8.5 18.5/13.5 18.5/3.5	GC D	Warm night temperature (18.5/13.5°C) strongly accelerated days to growth cessation, rate of growth cessation, depth of dormancy, rate of cold acclimation, depth of cold hardiness. Day temperature only influenced rate of dormancy development. Growth cessation, dormancy development and cold acclimation in 'Okanese' and 'Prairie Sky' were less affected by induction temperature than 'Walker' and 'Katepwa' suggesting that genotypic variations exist in response to temperature

Table 1 continued

Reference	Species	Source	Treatments		Response measures Growth Cessation (GC–height), Bud Set (BS—terminal bud), Endodormancy (D, evaluated through bud break)	Temperature response
			Photoperiod (h)	Temperature day/night (°C)		
Koski and Sievänen (1985)	*Pinus sylvestris* *Picea abies* *Betula pendula*	69°04′N—150 m ASL 68°01′N—280 m 63°18′N—105 m 61°48′N—90 m 59°25′N—45 m 53°07′N—140 m 47°09′N—360 m 41°59′N—240 m	Natural photoperiod	Heat sums from 1931 to 1960	GC BS	Consistent joint relationship between heat sum and night length for timing of GC. Trees were "flexible" in their timing of GC depending upon the year—and ranged more than 50 days between 1931 and 1960. The potential for predicting the growth of species using this model was discussed
Kramer (1957)	*Pinus taeda*	Eastern region of North Carolina	8	17/11 17/17 23/11 23/17 23/23 30/17 30/23	GC	Increased growth cessation when night temperatures increased under a 23°C day temperature. Growth was promoted under increasing day temperature and a constant 17°C night
Malcolm and Pymar (1975)	*Picea sitchensis*	8 Provinces from 59°50′N to 42°50′N	12, 16	8/5 12/7 16/9 20/11	GC BS	Northern provenances ceased growth under long days (16 h) and cooler night temperatures. Southern provenances required 12 h photoperiod and warm temperatures. Terminal bud development was advanced under warm temperatures
Mölmann et al. (2005)	*Populus tremula* × *P. tremuloides* and a PHYA overexpressor	T89 wild type clone Transgenic line PHYA22	12, 24	18/18 18/6	BS	Under short days (12 h), cool night temperature delayed BS. However under long days (24 h), only the cool night temperature in combination with paclobutrazol (GA biosynthetic inhibitor) induced bud set. Similarly in the PHYA22 overexpressing line, only the cool night temperature treatment alone or in combination with pacolobutrazol induced bud set
Palonen (2006)	*Rubus idaeus*	6 Cultivars	9, 18	4 20	GC D	Short days (9 h) in combination with warm temperature (20°C) enhanced growth cessation and induced deeper dormancy than low temperature

Table 1 continued

Reference	Species	Source	Treatments		Response measures Growth Cessation (GC–height), Bud Set (BS—terminal bud), Endodormancy (D, evaluated through bud break)	Temperature response
			Photoperiod (h)	Temperature day/night (°C)		
Partanen and Beuker (1999)	*Pinus sylvestris*	Ten ecotypes from 69°16′N to 62°30′N and from different altitudes (0–500 m)	Natural Photoperiod under greenhouse conditions at 61°48′N and 60°21′N	20/10°C Set point, but with widely varying temperatures. Temperature monitored hourly	GC BS	Response to temperature and photoperiod are under separate genetic controls. Photoperiod of the original site appeared to be the dominant factor in timing of GC
Søgaard et al. (2008)	*Picea abies*	9 ecotypes from 66°25′N to 54°05′N 1 and 2 year old seedlings	12	Constant 9 12 15 18 21	D	Strong interaction between temperature and duration of temperature treatment. 1 year old seedlings increased in depth of dormancy with increasing temperature while 2 year old seedlings peaked at 18°C
Svendsen et al. (2007)	*Cornus sericea*	62°N (NWT) and 42°N (Utah) ecotypes, 2 F1 families from reciprocal crosses and 191 F2 seedlings (NWT and Utah lines)	Field (natural conditions); Greenhouse (photoperiod matched to natural conditions of late summer and fall); and Phytotron (22, 8 h)	Greenhouse (20–25) Phytotron 20/15 15/5 20/5	D	Northern (62°N) but not southern ecotypes (42°N) could be induced into dormancy by long day (22 h) and cool temperature (20/5°C). In the F2 population, timing of dormancy induction was normally distributed with transgressive segregants for both early and late dormancy induction types. Greenhouse studies could not distinguish early and late dormancy induction types as clearly as field or phytotron environments and timing of dormancy induction under greenhouse conditions was delayed. A molecular marker linked to the low temperature-induced dormancy was identified
Van der Veen (1951)	*Populus alba,* *P. robusta,* *P. marylandica,* *P. tremula,* *P. trichocarpa,* *P. serotina,* *P. nigra,* *P. lasiocarpa*	Waginengen	16 9 16 12 24	30/20 30/20 18/14 18/14 22/22	GC BS	Warmer temperature treatment (30/20°C) slightly advanced GC and BS under short day (9 and 12 h) conditions in all species

Table 1 continued

Reference	Species	Source	Treatments		Response measures Growth Cessation (GC–height), Bud Set (BS—terminal bud), Endodormancy (D, evaluated through bud break)	Temperature response
			Photoperiod (h)	Temperature day/night (°C)		
Westergaard and Eriksen (1997)	*Acer platanoides*	5 Ecotypes:	Gradual reduction to 12 h and held	Constant	D	Warmer temperatures (18 > 14 > 10°C) induced a greater depth of dormancy
		60°10′N		18		
		59°05′N		14		
		56°45′N		10		
		55°45′				
		55°05′N				

Heide 1974, 2003; Malcolm and Pymar 1975; Jonkers 1979; Westergaard and Eriksen 1997; Junttila et al. 2003; Mölmann et al. 2005; Palonen 2006; Søgaard et al. 2008; Granhus et al. 2009; Kalcsits et al. 2009a, b, c). Heide (2003), for example, reported that warm autumn temperatures delayed spring bud break implying deeper dormancy levels under warmer autumn conditions. These studies are summarized in Table 1.

Although fewer studies have reported low temperature acceleration of GC, BS or D, consistent evidence indicates northern (but not southern) ecotypes, when combined with long photoperiods and cool temperatures will bypass the photoperiod requirement for these responses (Table 1, Dormling et al. 1968; Heide 1974; Malcolm and Pymar 1975; Junttila 1980, 1982; Downs and Bevington 1981; Mölmann et al. 2005; Svendsen et al. 2007). Håbørg (1972) reported night temperature was important for internode elongation and terminal dormancy. Even in crops that are photoperiodic-insensitive, GC (and endodormancy) was induced by cool temperatures (Heide and Pestrud 2005).

The relative importance of temperature regulation of the dormancy cycle is anticipated to profoundly increase with predicted climate change. The fall induction period appears to influence subsequent dormancy maintenance and release. Thus, understanding how temperature influences timing of growth cessation, induction dormancy and subsequent cold hardiness will be critical to plant adaptation. The models of Koski and Sievänen (1985) reinforce the importance of heat sum in combination with night length to jointly influence timing of growth in that the timing of GC varied by 50 days over a 29 year period.

In this paper, we take an initial step to address the seemingly contradictory responses of warm and cool temperature-induced dormancy and propose a working hypothesis of temperature-influenced dormancy induction in deciduous woody plant species. The possibility of temperature-mediated plasticity in growth cessation and dormancy development is intriguing because it identifies possible risk-adverse adaptations to ensure dormancy development under variable autumn temperatures. The underlying molecular and cellular mechanisms behind the two phenomena remain unclear and hypotheses will be proposed to identify areas of research physiologically separating these two proposed dormancy inducing processes.

Warm temperature-mediated, photoperiod-induced dormancy

The traditionally accepted factor inducing growth cessation and dormancy development in woody plants is short

Table 2 Pearson correlation coefficients between night and day temperature and growth cessation, dormancy 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^{ns}
Rate of growth cessation	0.721*	0.099^{ns}
Dormancy		
Rate of dormancy development	0.447^{ns}	−0.664*
Depth of dormancy	0.678*	-0.368^{ns}
Cold hardiness		
Rate of cold acclimation	−0.499*	-0.449^{ns}
Depth of cold hardiness	0.615*	0.303^{ns}

* $P < 0.05$, *n.s.* non-significant. From: Kalcsits et al. (2009a)

photoperiod. Recent evidence suggests temperature may mediate this process to a higher degree than originally thought and a review of the literature indicates that under short photoperiod (but not long photoperiod), warm temperatures have a consistently enhancing influence on G, BS and D in most woody plants of both northern and southern latitudinal origins (Table 1). As mentioned, Kalcsits et al. (2009a) reported night temperature had a greater influence than day temperature on most growth cessation and dormancy responses in poplar. This effect is currently not accounted for in existing growth models under future climate change conditions. The assumption that deciduous woody plants will be able to take advantage of the extended growing season during the autumn is currently being challenged. Furthermore, woody plants may actually stop growing earlier under warmer temperatures, which is directly opposite of current climate change growth models.

In our *Populus* study, the critical stages of growth, dormancy and cold hardiness were separated into components of: days to growth cessation, rate of growth cessation, rate of dormancy induction, depth of dormancy development, rate of cold acclimation, depth of cold hardiness (Table 2). Other than rate of dormancy development, night temperature, but not day temperature, was significantly correlated with all components. The more detailed breakdown of the results of three poplar clones are presented in Table 3 which widely differ in temperature sensitivity to dormancy induction: (1) Temperature insensitive dormant type (*P.* × 'Okanese'), (2) Temperature sensitive dormant type (*P.* × 'Walker') and (3) Temperature insensitive non-dormant type (*P.* × 'Prairie Sky'). Although 'Prairie Sky' appeared to enter dormancy, it was at such a slow rate that it was designated a non-dormant status.

These contrasting clones present a unique system with which to examine the impact of temperature on dormancy induction (Fig. 1). It is noteworthy that the temperature-insensitive and non-dormant type was still able to cease growth and cold acclimate (Kalcsits et al. 2009a). Temperature appeared to influence the rate of cold acclimation in this clone. Clearly, growth cessation is separate from

Table 3 Responses of three *Populus* hybrid clones differing in dormancy and dormancy sensitivity to temperature

Temperature regime (°C day/night)	Days to growth cessation (days)[1]	Rate of dormancy induction (ΔDBB day^{-1})[2]	Depth of dormancy (ΔDBB)[1]
Temp. insensitive dormant typel 'Okanese'			
13.5/8.5°C	29.7 ab	1.80 ± 0.21	28.8 a
18.5/3.5°C	30.6 b	1.00 ± 0.17	20.2 b
18.5/13.5°C	27.4 ab	1.20 ± 0.11	29.7 a
23.5/8.5°C	26.8 a	1.00 ± 0.05	27.0 a
Temp. sensitive dormant type 'Walker'			
13.5/8.5°C	34.5 b	2.60 ± 0.36	22.3 a
18.5/3.5°C	57.5 c	0.30 ± 0.07	6.3 c
18.5/13.5°C	28.2 a	2.00 ± 0.25	22.8 a
23.5/8.5°C	33.8 b	0.32 ± 0.05	10.3 b
Temp. insensitive non-dormant type 'Prairie Sky'			
13.5/8.5°C	35.2 b	0.20 ± 0.02	6.3 b
18.5/3.5°C	42.4 c	0.15 ± 0.03	5.1 b
18.5/13.5°C	27.4 a	0.24 ± 0.02	8.3 a
23.5/8.5°C	33.8 b	0.16 ± 0.01	6.6 b

Letters denote significant differences (at $\alpha = 0.05$) between treatments using Tukey's LSD test. Adapted from Kalcsits et al. (2009a)

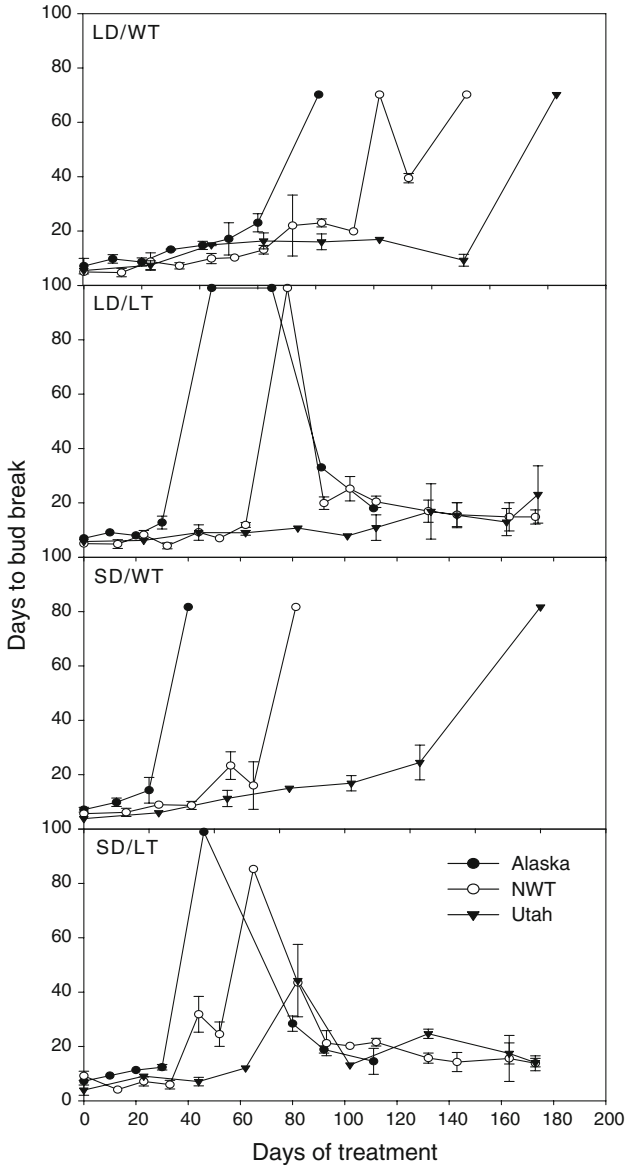

Fig. 1 Photoperiod and temperature studies on dormancy induction in Alaska (65°N), NWT (62°N) and Utah (42°N) under LD/WT (22/2 h, 20/15°C day/night), SD/WT (16/8 h, 20/15°C day/night), SD/LT (16/8 h, 15/5°C day/night), LD/LT (22/2 h, 20/5°C day/night with the 5°C occurring over 16 h). Days to bud break were measured under LD/WT conditions. From: Svendsen et al. (2007)

dormancy induction and furthermore it appears that a dormant state is unnecessary for cold acclimation. A different response was noted in the temperature-sensitive dormant clones. Here, it was depth of dormancy that was significantly influenced by temperature; warmer night temperatures and low day/night temperature differences induced the deepest dormancy. Using this type of system, where clones with differential response to temperature are used in conjunction with temperature treatments allows for the disassociation of the clonal and environmental effects.

Low temperature-induced dormancy

In contrast to the observations in hybrid poplar, using northern and southern ecotypes of dogwood, low temperature under long photoperiod induced dormancy development in northern ecotypes but not southern ecotypes (Fig. 1). Notably, the low temperature treatment under short days also accelerated dormancy induction in southern ecotypes but the combined SD/LT combination did not further accelerate dormancy induction in northern ecotypes. The higher the day/night temperature difference and the lower the night temperature, dormancy was more quickly induced in the northern ecotypes and a molecular marker associated with the cool temperature dormancy response was identified in the F2 segregating populations (Svendsen et al. 2007).

These observations are consistent with GC, BS or D responses reported by various researchers on northern ecotypes. Dormling et al. (1968) reported the northern ecotype of *Picea abies* was induced into GC and BS at the same date under either LD (24 h) or SD (16 h) and cool temperature (10°C) treatment. Cool temperature treatments under long or short days also induced a deeper dormancy compared to warm temperature and a short day in this northern ecotype. In *Picea abies*, long day and cool temperature conditions induced GC in all ecotypes with the northern-most ecotypes (L1, A2, F1) the most responsive (Heide 1974). In *Picea sitchensis*, Malcolm and Pymar (1975) found northern provenances ceased growth under long days (16 h) and cooler night temperatures while southern provenances required 12 h photoperiod and warm temperatures. Junttila (1980, 1982) examined photoperiod and temperature GC responses of *Betula pubescens* (1980) and *Salix pentandra* (1980, 1982) and found GC was induced earlier under fluctuating lower night temperatures than constant temperatures particularly in the northern ecotypes under long photoperiods. Downs and Bevington (1981) found northern ecotypes of *Betula papyrifera* increased BS with long days and decreasing temperature but had no influence in southern ecotypes. In the wild type and transgenic poplar (*PHYA* overexpressor), under short days (12 h), cool night temperature delayed BS (Mölmann et al. 2005). However, under long days (24 h), only the cool night temperature in combination with paclobutrazol (GA biosynthetic inhibitor) induced bud set.

Mechanisms of warm and low temperature-mediated dormancy induction

Multiple pathways likely exist that regulate bud set: a low temperature-induced stress pathway of northern ecotypes and a warm night temperature-short-photoperiod induced

Table 4 Percentage bud break in Alaska and Utah ecotypes after a 30 day exposure to the photoperiod and temperature treatments and 20 days under long day (22 h) and warm temperature (23°C) bud break conditions

Treatments	Alaska	Utah
LD/WT	100	100
LD/LT	62	100
SD/WT	70	100
SD/LT	45	100

LD/WT: 22/2 h photoperiod, 23°C/23°C (day/night)

LD/LT: 22/2 h photoperiod, 23°C/5°C (with 5°C low temperature over 16 h beginning with the night period)

SD/WT: 8/16 h photoperiod, 23°C/23°C (day/night)

SD/LT: 8/16 h photoperiod, 23°C/5°C (day/night)

* $P < 0.05$, *n.s.* non-significant

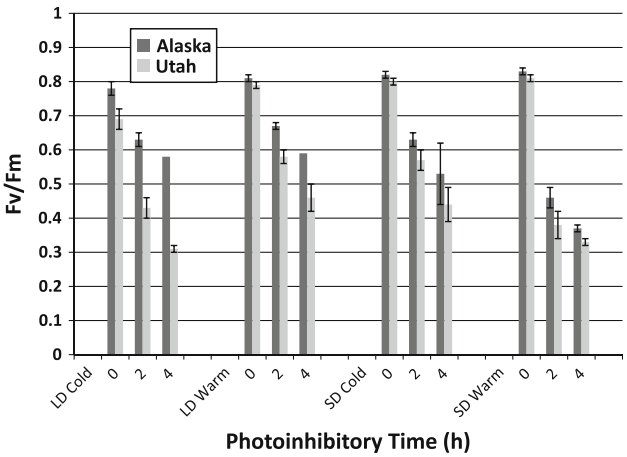

Fig. 2 Photoinhibitory responses in leaves of Alaska and Utah ecotypes of dogwood (*Cornus sericea* L.). All determinations were performed 30 days after shifting to the conditions indicated for the induction of dormancy. Photoinhibition occurred at 4°C and 1200 µmol photons m^{-2} s^{-1}. Responses were estimated by the Chl fluorescence parameter F_v/F_m and determined using a PAM-2000 modulated fluorometer. Long Day (LD), Short Day (SD), Low Temperature (Cold) and Warm Temperature (Warm) treatments as per Fig. 1

pathway which impacts all ecotypes. Under field conditions, the two processes of warm and low temperature-mediated dormancy induction may occur in concert to promote rapid cessation of growth and/or induction of dormancy in late summer or autumn and therefore, overlapping effects may be present. The underlying changes in molecular function that result in these contradictory responses can be separated into two sections; the signaling network and the downstream cellular and molecular responses to plant signals.

Signalling network

Abiotic stresses can increase the rate of bud set to provide protection against unfavourable conditions in some species. Photooxidative stress is induced under the combination of low temperature in the presence of light (Öquist and Huner 2003; Ensminger et al. 2006). Alaska and Utah ecotypes differentially responded to dormancy inducing conditions of temperature and photoperiod (Table 4). Both the long day and short day/low temperature combination (LD/LT, SD/LT) induced a greater degree of dormancy in Alaska than Utah. We found under long-day conditions, the Alaska ecotype was more tolerant to photoinhibitory treatment than the Utah ecotype (Fig. 2). This was more pronounced under low temperature (LD/LT) conditions. The ecotype differences in photoinhibitory responses were minimized under short-day conditions, irrespective of temperature. Both ecotypes possess an active xanthophyll cycle as evidenced by the conversion of violaxanthin to zeaxanthin upon photoinhibition but the Alaska ecotype demonstrated an increase in constitutive xanthophyll pool size under all growth conditions in comparison to the Utah ecotype (data not shown). These results suggest the northern Alaska ecotype may be able to maintain higher photosynthetic efficiency with reduced photoinhibition under LD/LT conditions.

Low temperature stress-induced growth cessation may occur under long day conditions. In adapted northern ecotypes, this low temperature-mediated dormancy induction may result in true endodormancy by allowing photosynthesis to continue under LD/LT conditions rather than inducing only a growth cessation response due to photooxidative stress. Day/night temperature shifts primarily induce alterations in net carbon accumulation (see Öquist and Huner 2003; Ensminger et al. 2006). Simple sugars such as sucrose increase dramatically in cells in response to low autumn night temperatures (Levitt 1980) and accumulating evidence indicates sucrose may be acting as a signaling molecule (Horvath et al. 2002). Dijkwel et al. (1997) reported sucrose controlled phytochrome A (PhyA) signaling in *Arabidopsis* and PhyA is appears to regulate bud dormancy induction in poplar (Olsen et al. 1997) and aspen (Eriksson 2000). Kim et al. (2002) also showed phytochrome B (PhyB) was the primary photoreceptor responsible for the activation of cold-stress signaling to light in *Arabidopsis*. Additionally, Short (1999) reported that the presence of sucrose was required, and in combination with an overexpression of PhyB, inhibited PhyA function in *Arabidopsis*.

While its sensitivity to light has been the focus of the majority of studies, phytochrome has also been clearly shown to be temperature-sensitive (see Hennig 2006 for a review on phytochrome degradation and dark reversion). Both dark reversion of P_{fr} to P_r in yeast (Schäfer and

Schmidt 1974; Hennig and Schäfer 2001) and phytochrome P_{fr} destruction in maize coleoptiles (Butler and Lane 1965) were temperature-dependent with warm temperature accelerating the conversion of P_{fr} to P_r. Conceivably, responses which are regulated by the P_r:P_{fr} ratio may be affected by changes in environmental temperature, particularly night temperature. An important new finding is the function of PIFs (PHYTOCHROME-INTERACTING-FACTORS) and its relation to temperature. The P_{fr} form of phytochrome is transported to the nucleus when exposed to light and combine with PIFs to promote gene expression (Castillon et al. 2007). Ruttink et al. (2007) found PIF4 and PIF3-LIKE1 genes elevate soon after dormancy-inducing short day exposure in *Populus* trees. Interestingly, Stavang et al. (2009) recently showed a temperature-influenced PIF4 expression in *Arabidopsis*.

In *Arabidopsis,* Böhlenius et al. (2006) indicated the poplar ortholog (PtFT1) of the *FLOWERING TIME LOCUS* (FT) gene was induced by the poplar *CONSTANS* (PtCO2) gene and controlled growth cessation and dormancy in *Populus tremula* × *tremuloides* ecotypes. The PtFT1 expression inhibited growth cessation and dormancy development. Under long photoperiods, PtCO2 expression peaks after dawn and induces PtFT1. This response is dependent upon its latitudinal adaptation. Peak expression seems to be mediated partially by Phy A in the evening and PhyB in the morning (Valverde et al. 2004). Under short photoperiods, PtCO2 peaks at night and thus fails to induce PtFT1. At night, *SUPRESSOR OF PHYA* (SPA-family genes) controls expression of CO. The regulation of the FT gene in *Arabidopsis* is also involved the interaction between PhyB and temperature (Halliday et al. 2003). Temperature altered flowering time in *Arabidopsis*, controlled by the P_r:P_{fr} ratio of PhyB. Since temperature affects the expression of the FT gene in *Arabidopsis*, temperature may potentially also modify the expression of PtFT1 in woody plants.

Interesting information on DORMANCY-ASSOCIATED MADS-BOX (DAM) genes is revealed using an herbaceous perennial weed, leafy spurge (Horvath et al. 2009a, b). In this plant, DAM genes are induced by low temperature and the authors hypothesize the DAM genes induce dormancy through negative-regulation of FT or FT-like genes (Horvath et al. 2009a). Furthermore, Foley et al. (2009) reported decreasing temperatures prior to vernalization were required for flowering competence in leafy spurge, and decreasing photoperiod and vernalization alone were insufficient. Two of the DAM transcription factors are targeted in the meristematic cells and binding sites of the potential regulatory elements, CBF (low temperature) and EVENING (circadian rhythm) were identified on the DAM genes (Horvath et al. 2009b). It may be fruitful to examine and compare DAM genes in northern and southern ecotypes or clones of contrasting temperature responses.

Phytohormones have long been associated with regulating various aspects of the dormancy cycle (see Tanino 2004 for a review). Temperature-regulated-hormone-mediated growth and dormancy induction has been largely associated with GA biosynthesis, particularly in relation to thermoperiodism. Moe (1990) suggested the observed differences in growth and stem elongation under high day/night temperature alterations was a result of changes to GA sensitivity and metabolism. Specifically, daily temperature fluctuations affected the endogenous level of bioactive GA_1 in the stems. A positive day–night temperature difference (positive DIF) increases GA_1, GA_{12}, GA_{19} and GA_{20} concentrations in *Begonia* × *hiemalis* Fotsch (Myster et al. 1997). Positive DIF resulted in less 2β-hydroxylation of bioactive GA_1 to inactive GA_8 than negative DIF (higher night than day temperatures) in *Pisum sativum* (Grindal et al. 1998).

Many reports indicate endogenous gibberellins (GA) concentration correlate with stem elongation and growth cessation (Jansen et al. 1986; Juntilla et al. 1991; Olsen et al. 1995; Mölmann et al. 2003) in woody plants. In addition, GA concentrations decreased upon exposure to short photoperiod in willow trees (Junttila and Jensen 1988). In their 2002 paper, Horvath et al. hypothesized that sugar produced in leaves inhibited leafy spurge underground buds through negative regulation of GA biosynthesis or signal transduction.

For an excellent review of temperature perception and signal transduction in plants, the readers are referred to Penfield (2008). It is becoming more apparent that signaling is a series of highly dynamic pathways that do not contribute to linear responses in plants. The division of signaling networks into growth promoting and growth inhibiting networks may be the distinction between photoperiod- and stress- induced dormancy induction.

Downstream cellular and molecular response to plant signals

Ultimately, growth cessation and dormancy control revolve around regulation of meristematic activity (Rohde and Bhalerao 2007) within woody plants. The cell cycle has a significant impact on dormancy through its regulation of meristem activity (see Horvath et al. 2003 for a review). Horvath et al. (2002) found sugar, auxin and GA all acted at different points of the cell cycle in controlling underground bud growth and development in leafy spurge. The influence of phytohormones such as ABA on the cell cycle (Rohde et al. 1997; LeBris et al. 1999) may be directly mediated by temperature through stress responses. Potentially, the long photoperiod and low temperature-induced GC, BS and D responses in northern but not southern

Table 5 Correlation coefficients between dormancy and ADC and T_1 relaxation times within various Regions of Interest

Region of Interest (ROI)	ADC	T_1 Relaxation times
Stem vascular region	−0.79**	−0.65*
Vascular transition region	−0.90***	−0.36
Lateral bud	−0.92***	−0.25

Significance * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

From: Kalcsits et al. 2009b

ecotypes could be associated with a combined ABA stress/sucrose signaling network enhanced through higher tolerance to photoinhibition. However, these aspects have not yet been explored.

Understanding is also lacking on how this control is applied. Under a short photoperiod, in lateral buds of poplar clones with contrasting responses to temperature, we examined water mobility and binding at a tissue-specific level using non-destructive magnetic resonance micro-imaging (MRMI; Kalcsits et al. 2009b). Water mobility decreased in association with short day, temperature-mediated dormancy induction in lateral buds. This implies that changes in water mobility are closely related to photoperiod-induced dormancy and temperature can modulate this process. Water mobility, quantified as the apparent diffusion coefficient (ADC), significantly decreased with increases in dormancy levels in both contrasting temperature sensitive axillary buds in these poplar clones. This measure was more closely correlated with dormancy development than the more commonly measured T_1 relaxation coefficient (Table 5) over all temperature induction treatments. Water diffusivity or mobility is less commonly measured but represents a more dynamic measure of water activity accessible using MRMI technology (Hou et al. 1997; DeFay et al. 2000; Van der Toorn et al. 2000). Tissue-level changes in water in lateral buds during photoperiod-induced dormancy induction suggest that control of dormancy may be related to restrictions of tissue and cellular water movement.

Two processes that regulate water status in the cell are water binding and tissue dehydration. Accumulation of hydrophilic molecules may bind water and restrict its movement within plant tissue and may be associated with dormancy induction (Faust et al. 1995; Erez et al. 1998). In addition to biophysical interactions between water and hydrophilic/hydrophobic molecules, restriction of movement both in and out of plant tissue may regulate dormancy status in vegetative buds such as the lack of xylem differentiation into the bud (Ashworth 1982). Water is largely transported between cells through the plasmodesmata and aquaporin water channels and may be reduced during dormancy induction by blockage of the plasmodesmata through differential calcium deposition (Jian et al. 1997) or by 1-3-β-glucan (Rinne et al. 2001; Rinne and Van der Schoot 2003). Although indirect, there are examples of higher accumulation of 1-3-β-glucan in bean (*Phaseolus vulgaris*) under warmer temperatures (Abeles and Forrence 1970). Therefore, more rapid accumulation of 1-3-β-glucans during warm temperature-enhanced dormancy induction could occur.

Yooyongwech et al. (2008) also reported changes in both water status and aquaporin gene expression, particularly in the basal portion of the bud during peach dormancy induction. Molecular work exploring temperature-influenced blockages and aquaporin activity would contribute to understanding changes in intercellular water mobility and subsequently, warm and low temperature-induced dormancy.

Working hypothesis of two distinct dormancy-inducing pathways in deciduous woody plants

We propose two distinct dormancy-inducing pathways in northern ecotypes of woody plants; a low temperature-stress-induced and a warm temperature-photoperiod-induced pathway. These apparently redundant adaptations may ensure dormancy development and cold acclimation under both unseasonable conditions and more favourable, moderate temperatures. In years where the onset of cold temperatures is later than normal, warm temperature-photoperiod-induced dormancy may play a greater role in growth cessation and dormancy induction. This ensures plants at northern latitudes will be plastic in their ability to maximize their growing season while reducing the risk of winter injury from late acclimation due to delayed growth cessation.

From our work, we have presented evidence of this hypothesis in two different plant systems. However, research is required to elucidate the underlying molecular mechanisms driving these two processes to determine whether there are indeed two pathways in deciduous woody plants from northern latitudes or whether one pathway is variably expressed in response to different environmental conditions. Particular attention needs to be paid to molecular mechanisms that restrict inter- and intracellular water movement in lateral and apical buds, temperature-linked hormonal regulation of the cell cycle, stress-induced growth response genes, the influence of temperature on photosynthetic efficiency and P_{fr} conversion, as well as an assessment and regulation of DAM genes in northern and southern ecotypes of woody plants.

The significant interactions between photoperiod × temperature (day and night) × population (latitudinal and altitudinal) will impact the ability of species to

move northward into longer photoperiods under anticipated temperature shifts under climate change. That the northern ecotypes may have a distinct dormancy induction mechanism than southern ecotypes is promising because it represents a new step towards understanding the complexity of dormancy and articulating the varied temperature-induced responses. Phenotypic plasticity is important in harsh, unpredictable climates and addressing how plants have adapted to maximize growth and reproduction while minimizing stress injury is critical to understanding how winter damage risk changes in response to changing environmental conditions.

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