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## ORIGINAL ARTICLE

# Spring bud phenology of 18 *Betula papyrifera* populations in British Columbia

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### Abstract

Paper birch (*Betula papyrifera* Marsh.) is an ecologically valuable and suitable new reforestation species in British Columbia (BC). An understanding of birch's genecology is important to deploy it successfully. Eighteen paper birch populations (49–55°N) were collected from five distinct geographic regions in BC to determine whether observed variability in spring bud phenology was due to genetics, the growing environment or their interaction. Seedlings were grown at three common gardens in Prince George (53°45'N), Salmon Arm (50°47'N) and Victoria (48°29'N) to observe the bud break. Further a controlled photoperiod, a root zone temperature and a translocation experiment from the northern to central garden were conducted to investigate the effect of photoperiod and root temperature on birch bud break. Results revealed that timing of spring bud phenology in paper birch is under genetic and environmental control, following climatic clines based on latitude from south to north. Bud flush at the southern common garden was on an average 25 days earlier and required 177 more growing degree day than the northern common garden. Conversely, our controlled experiments and seed source translocation experiment showed that the signal for the onset of spring bud flush is controlled by air temperature, soil temperature, and photoperiod. These results allow us to characterize spring budburst phenology of paper birch and begin to consider seed zones and seed zone transfer guidelines for BC.

**Keywords:** Birch, bud break, dormancy release, growing degree day (GDD), photoperiod, translocation experiment.

### Introduction

Paper birch (*Betula papyrifera* Marsh.) is an early-seral species found on productive sites occupying a range of environmental conditions from low to mid elevation in the interior of British Columbia (BC) (Benowicz et al., 2001; Carlson et al., 2000). In addition to increased acceptance of birch as a suitable reforestation species (Carlson et al., 2000), there are predictions that climate envelopes in BC suitable for good birch growth will increase 64% by 2025 (Hamann & Wang, 2006). In order to respond to these events, a better understanding of the genecology of paper birch is needed.

From different studies, it has been shown that tree growth is enhanced when seed sources are moved northward (Farmer, 1993; Viherä-Aarnio & Velling, 2008) and this is where most of the range increase in BC for paper birch is predicted to occur (Hamann &

Wang, 2006). Over time, tree species have developed ecotypes that are adapted to local climatic conditions (Li et al., 2003; Pudas et al., 2008). Transfer of sources to new environments, a potential mismatch between life cycle and seasonal climate fluctuations, may predispose species to frost damage or growing season injury (Cannell & Smith, 1986; Viherä-Aarnio & Velling, 2008).

Monitoring of vegetative bud break phenology may be one of the better way to assess a population's suitability to new environments (Leininen & Kramer, 2002; Linkosalo et al., 2006). Bud break is useful for screening clones and progenies in tree breeding programs since it can be easily observed in springtime (Hannerz, 1999). Bud flush is part of the annual growth cycle which is regulated by environmental factors such as temperature and day length (Heide, 2008; Myking & Heide, 1995). Spring bud break is considered to be regulated by air

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temperature in two ways: (1) Provide the chilling temperatures to end dormancy (Perry, 1971). Dormancy is a resting period where buds remain dormant even if they are exposed to growing conditions (Hänninen, 1990). (2) Once chilling needs are met, provide the heat or favorable growth conditions to allow ontogenetic development (Hänninen et al., 2007; Linkosalo et al., 2008). The dormancy release is controlled by the fulfillment of chilling requirement which usually involves temperatures  $\leq 5^{\circ}\text{C}$  for few weeks (Cannell & Smith, 1983). However, chilling requirements are varied with the change of provenance's latitude. According to Hannerz et al. (2003), northern provenances of *Picea abies* (L.) H. Karst. require less chilling than the southern provenances. Moreover, long night may also promote the dormancy release in species like *P. abies* (Qamaruddin et al., 1993). However, no direct relationship has been established between time of dormancy release and timing of spring bud break (Heide, 1993).

It has also been suggested that fall temperatures during dormancy induction influence spring bud break: plants maturing at warmer temperatures in the fall enter a deeper state of dormancy and exhibit a delay in spring bud break (Granluis et al., 2009; Sogaard et al., 2008). This increases the chilling requirement especially for *Alnus glutinosa* (L.) Moench *Betula pendula* Roth and *Betula pubescens* Ehrh (Heide, 2003; Myking & Heide, 1995). Although fall air temperatures explain more of the variation in spring bud breaks (*B. pendula* and *B. pubescens*) (Heide, 2003) but spring air temperature may also play an important regulatory role for *B. pendula* (Linkosalo et al., 2006) *B. pubescens* (Pudas et al., 2008) and many other temperate species (Wielgolaski, 2001).

In addition to temperature, photoperiod has been implicated as having a regulatory role in spring bud break in many species such as *B. pendula* and *B. pubescens* (Myking & Heide, 1995) *P. abies* (Partanen et al., 2005) and *Prunus* species (Heide, 2008). However, others have suggested photoperiod has no role in spring bud break (some northern hardwood trees) (Hunter & Lechowicz, 1992) while some mentioned that the role of photoperiod is species specific (Schaber & Badeck, 2003) or even specific to populations within a species (*Pseudotsuga menziesii* [Mirb.] Franco) (Irgens-Moller, 1957). Clearly the role of photoperiod in relation to spring bud break needs elucidation.

Regardless of the mechanisms controlling spring bud break, general observations in common gardens indicate northern and high-elevation populations or ecotypes (*Betula alleghaniensis* Britt.; *Betula lenta* L.; *Populus balsamifera* L.; *B. pubescens*) require less heat

to flush than do southern or low elevation ecotypes and thus begin growth earlier (Farmer, 1993; Pudas et al., 2008; Sharik & Barnes, 1976). Furthermore, interior or continental populations (*Ulmus glabra* Huds.) require less heat to break bud than do coastal populations (Myking & Skrøppa, 2007). While considerable works have been done on birch genealogy and phenology in Europe (Li et al., 2003; Myking & Heide, 1995; Pudas et al., 2008; Rousi & Heinonen, 2007; Viherä-Aarnio & Velling, 2008), to date, little attention has been given to birch in North America and few works have been published yet (Benowicz et al., 2001; Sharik & Barnes, 1976; Simpson et al., 2000).

We have studied the variability of spring bud phenology of paper birch populations from a range of latitudinal origins. The objectives of the investigation were to determine the critical environmental regulatory factors such as: role of photoperiod and temperature (air and soil) during flushing and the role of latitudinal transfer on bud flush.

## Materials and methods

### Common garden experiment

In 1994, seed was collected from 10 paper birch trees with good form in each of 18 populations covering five distinct climatic regions in the BC interior (Carlson et al., 2000, Figure 1, Table I). The regions ranged from dry and cold to warm and wet (Table II). Seedlings were grown in 1995 at Kalamalka Forestry Centre ( $50^{\circ}14'\text{N}$  and  $119^{\circ}16'\text{W}$ ) in 415D styroblocks (Beaver Plastics, Edmonton, AB) and planted into three common gardens in the spring of 1996 after over wintering in cold storage (Carlson et al., 2000). The gardens were located at Victoria, BC (southern and coastal;  $48^{\circ}29'\text{N}$  and  $123^{\circ}24'\text{W}$ ), Skimikin, BC (central and interior;  $50^{\circ}47'\text{N}$  and  $119^{\circ}24'\text{W}$ ), and Prince George, BC (northern and interior;  $53^{\circ}45'\text{N}$  and  $122^{\circ}43'\text{W}$ ). In total, six seedlings per provenance were planted at  $2\text{ m} \times 2\text{ m}$  spacing in a randomized block design [30 trees per seed source planted as six trees in each of five replications]. This allows for comparisons among biogeoclimatic regions, seed sources within biogeoclimatic regions, and among common gardens.

After acclimation to the sites, spring bud phenology was assessed in every second day at the three garden locations between 1998 and 1999. The date of bud burst was defined as "when the first green ragged edges visually appear between the bud scales, almost like the opening of a clam shell" (Berger, 2001). A minimum of 10 buds were assessed on a branch in the upper crown of at least 24 trees per

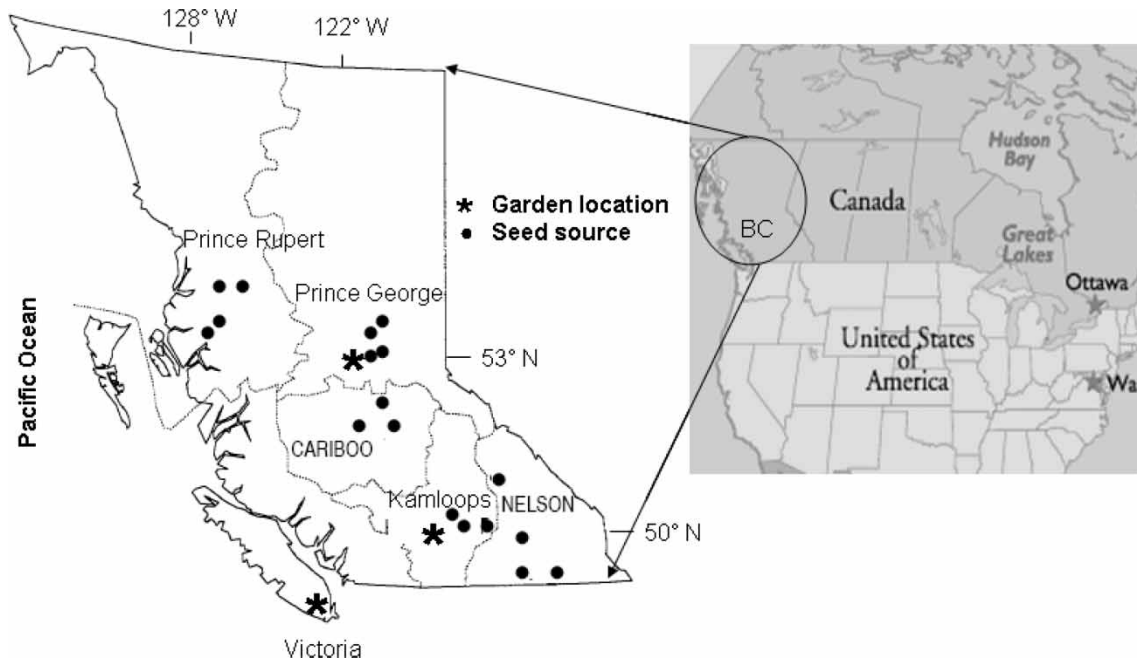


Figure 1. Location of Birch provenances and common gardens.

population at the northern and central gardens and a minimum of 10 buds on at least 10 trees per population at the southern garden.

Temperature data for each garden location were acquired from the nearest weather station to calculate the growing degree days (GDD) or heat sum.

Table I. Geographic origin and climatic variables of different paper birch seed sources and trial locations.

Region	Name	Code	Latitude (N)	Longitude (W)	Elevation (m)	MAT	MTCM	TD	DD > 5	DD > 5 <sub>100</sub>	FFP
Nelson	Porcupine Ck <sup>a</sup>	1	49°15'	117°10'	840	4.9	-6.7	23.1	1424	129	110
Nelson	St Mary River	3	49°38'	116°03'	990	4.3	-8.2	24.7	1373	133	101
Nelson	Wilson Ck <sup>a</sup>	5	50°04'	117°23'	915	5.0	-7.0	23.6	1454	128	108
Nelson	Mars Ck	7	51°22'	118°18'	990	3.5	-9.0	24.0	1216	135	95
Kamloops	Barnes Ck	9	50°34'	118°50'	850	5.1	-6.3	22.5	1419	128	109
Kamloops	Lee Ck <sup>a</sup>	11	50°46'	119°32'	600	5.8	-6.0	22.9	1599	121	115
Kamloops	Bush Ck <sup>a</sup>	13	50°49'	119°45'	1250	3.8	-7.3	22.5	1220	137	91
Cariboo	Cuisson Lk <sup>a</sup>	15	52°31'	122°24'	760	4.7	-7.2	23.1	1402	126	103
Cariboo	Raft Ck <sup>a</sup>	17	52°31'	121°31'	830	3.8	-8.0	22.6	1187	134	86
Cariboo	Sardine Ck	19	52°47'	122°14'	760	4.0	-8.8	23.9	1256	132	96
Prince George	Frost Lk	21	53°47'	122°38'	975	2.9	-9.8	24.1	1114	137	87
Prince George	Tabor Lk	23	53°55'	122°22'	915	2.7	-9.8	23.8	1072	139	82
Prince George	Eaglet Lk <sup>a</sup>	25	54°06'	122°21'	685	3.4	-10.8	26.0	1259	133	95
Prince George	Amanita Lk <sup>a</sup>	27	54°08'	121°47'	760	3.1	-10.7	25.5	1199	135	90
Prince Rupert	Skeena River	29	54°30'	128°34'	70	6.5	-3.9	20.1	1568	121	152
Prince Rupert	Little Oliver Ck	31	54°42'	128°16'	270	5.9	-4.1	19.0	1374	124	134
Prince Rupert	Juniper Ck <sup>a</sup>	33	55°08'	127°43'	350	5.5	-6.6	22.6	1508	122	131
Prince Rupert	Burdich Ck <sup>a</sup>	35	55°11'	127°47'	480	4.1	-8.0	23.0	1219	134	100
<b>Experiment trial location</b>											
South garden	Victoria	3	48°29'	123°24'	20	10.2	4.2	12.7	2126	—	236
Central garden	Skimikin	2	50°47'	119°24'	560	6.2	-5.6	23.0	1684	119	124
North garden	Prince George	1	53°45'	122°43'	630	4.2	-8.9	24.8	1369	130	106
Compound	UNBC EF lab		53°54'	123°49'	780	3.0	-9.3	23.3	1082	82	81

Mean annual temperature (MAT); mean temperature of the coldest month (MTCM); continentality or extreme temperature difference (TD); degree days above 5°C (DD > 5); Julian day when 100 degree days at 5°C base occur (DD > 5<sub>100</sub>) and frost free period (FFP) Climate BC Model (<http://genetics.forestry.ubc.ca/cfgc/ClimateBC/>) – accessed 25 February 2011 based on year 1971–2000.

<sup>a</sup>Provenance used for photoperiod, warm and cold root experiment.

Table II. Climatic parameters for birch seed source home regions. Compiled from Meidinger and Pojar (1991).

Region	Seed code	BEC	MAT range (°C)	Number of months <0°C	MAP range (mm)	Number of months >10°C
Prince Rupert (PR)	29	CWH	5.2–10.5	0–2	1000–4400	4–6
	31–35	ICH <sup>a</sup>	2.0–8.7	2–5	500–1200	3–5
Prince George	21–27	SBS	1.7–5.0	4–5	440–900	2–5
Cariboo	15–19	IDF <sup>c</sup>	1.6–9.5	2–5	300–750	3–5
Kamloops	9–11	IDF <sup>d</sup>	1.6–9.5	2–5	300–750	3–5
	13	MS	0.5–4.7	5	380–900	2–4
Nelson	1–7	ICH <sup>b</sup>	2.0–8.7	2–5	500–1200	3–5

BEC, biogeoclimatic zone; CWH, coastal western hemlock; ICH, interior cedar hemlock; SBS, sub boreal spruce; IDF, interior Douglas-fir; MS, montane spruce.

MAT, mean annual temperature; MAP, mean annual precipitation based on last 30 years.

<sup>a</sup>PR, ICH colder end of temperature and drier end of precipitation.

<sup>b</sup>Nelson ICH warmer end of temperature and wetter end of precipitation.

<sup>c</sup>Cariboo IDF colder end of temperature range and wetter end of precipitation.

<sup>d</sup>Kamloops IDF warmer end of temperature range and drier end of precipitation.

The GDD were calculated based on mean daily temperature starting on 1 February of each year because there was no or little heat accumulation in December and January at interior sites (Central and Northern garden location). The GDD was calculated based on the following formula:

$$\text{GDD} = \sum [(T_{\max} + T_{\min})/2 - T_{\text{thres}}] \quad (1)$$

(If  $T < T_{\text{thres}}$  then heat sum = 0 and  $T > T_{\text{thres}}$ )

Where  $T_{\max}$  are the maximum and  $T_{\min}$ , minimum temperatures recorded over each 24-h period,  $T_{\text{thres}}$  is the threshold temperature. The threshold temperature was 0°C (Heide, 1993; Pellis et al., 2004; Rousi & Pusenius, 2005). If GDD calculations had been initiated on 1st or 15th January for the southern garden, GDD would be greater by 153 or 127 units, respectively, for that garden. In the central and northern gardens there were no GDD between 1 and 15 January but there were 24 and 12 GDD, respectively, from the 15 to 31 January. Day length was calculated on 21 of each month for each population and garden using the US Naval Observatory tables (<http://www.weatherimages.org/latlon-sun.html>). The different climatic variables were estimated for each population by using Climate BC Version 3.2 (Wang, 2006, <http://www.genetics.forestry.ubc.ca/cfcg/climate-models.html>)

#### Translocation experiment from north to central garden

To identify if photoperiod has any regulatory effect on bud break a translocation experiment was conducted. At the time of trail establishment in spring 1996, approximately 15 trees from each seed source were potted in 4 L plastic pots at the northern garden for translocation to the central common garden. The pots were buried in sawdust adjacent to trees in the northern common garden (Table I). On 4 and 5 March of 1999 when the effective

photoperiod (day length + civil twilight) was 12 h, five pots from each source were translocated from the northern garden to the central garden to observe completion of spring phenology event. The potted trees remaining in the northern garden and those transferred to the central garden were monitored for spring bud break. The chilling days were based on mean daily temperatures between +5 and –2°C from beginning of October. The amount of chilling for a day was equal to the mean daily temperature. At the time of transfer from north to south the chilling days were 253.2 and accumulated GDD 18.3. However by the end of March, chilling days had increased by 83.3 and 65.3, respectively, at the central and northern gardens while GDD had increased by 89.5 and 36.5, respectively.

#### Photoperiod experiment

To study the effect of photoperiod on bud break, 10 populations, two from each of the five climatic regions (Nelson = Porcupine Ck and Wilson Ck; Kamloops = Lee Ck and Bush Ck; Cariboo = Cuisson Lk and Raft Ck; Prince George = Amanita Lk and Eaglet Lk; Prince Rupert = Juniper Ck and Burdich Ck) were used (Table I). Samples from five trees from each population were collected in 1998. These were grown in a container nursery in 1999, and after cold storage, planted into 4.5 L pots in the spring of 2000 at Prince George (53°54'N latitude; 122°49'W longitude) and placed under irrigation in an outdoor compound. In September 2000 these were buried outdoors in sawdust.

On 8 January and again on 20 February 2001, five trees from each population were placed in two controlled environments: long days (LD) 16/8 h D/N and short days (SD) 8/16 h D/N with 21°C day temperature and 12°C night temperature. Phenology assessments were done every second day. All

populations were returned to the irrigated UNBC green house outdoor compound in May 2001 for next season cold and warm root treatment experiment.

#### *Cold and warm root temperature experiment*

After returning to the UNBC green house compound all potted trees were buried in sawdust in September 2001. On 15 February 2002, 10 trees from each of 10 populations (Table I), half of which had received standard deviation (SD) treatment and half the LD treatment in 2001, were placed in two root environments: warm roots with mean temperature  $13.8 \pm 1.2^\circ\text{C}$  (SD) and cold roots (CR)  $0.8 \pm 0.7^\circ\text{C}$ . Air temperature was set to D/N of 18/10° C and averaged 16.4/10.5° C during the study under a 15/9 h D/N photoperiod regime. Rooting zone temperatures were monitored continuously. The CR experiment was maintained by placing snow around the pots every second day.

#### *Statistical analysis*

A general linear model (GLM) with an analysis of variance (ANOVA) was conducted using SYSTAT® (version 12.0). We were unable to use repeated ANOVA due to the unequal sampled size between the years. The effect of altitude on bud break was not investigated since in a previous study Balliet (2009) reported that bud break did not significantly advance from lowest elevation to highest elevation for a common garden provenance trial conducted using the same experimented area. A similar result was also demonstrated by Sharik and Barnes (1976) where they found an absence of differentiation amongst populations from different elevations.

All statistical analysis was conducted based on 50% bud break where seed source and region were main effects to differentiate among the seed sources and regions. To study the differentiation of regional grouping, all 18 populations were pooled to form five climatic regional groups (Table II) (Nelson [South east], Kamloops [South Central], Cariboo [Central], Prince George [North Central], and Prince Rupert [North West]) and were analyzed with ANOVA. However, both seed sources and region showed a similar result with respect to significance and *F* values. Further a nested ANOVA analysis was conducted where seed sources nested within region (independent variable) for Julian days (JD) and GDD (dependent variable). The variance components and significance for this model were estimated with GLM procedures. Finally, region was considered as a main effect to describe the geographic variation for paper birch seed sources as region may have wider implication in seed zones and

seed transfer guidelines preparation. The final ANOVA model used in the analysis was:

$$B_{50\%} = m + G + R + G \times R + S(R) + \varepsilon \quad (2)$$

Where *B* is the bud break proportion (50%), *G* the garden factor, *R* the region factor, *S* seed source factor, which is nested within factor region (*R*), and  $\varepsilon$  is the error term. The same model (2) was also used to analyze the translocation experiment. Further ANOVA was conducted to study the impact of different photoperiods and root temperatures on birch bud break in seed sources as well as climatic regions.

$$B_{50\%} = m + T + R + T \times R + S(R) + \varepsilon \quad (3)$$

Where *B* is the bud break proportion (50%), *T* the treatment factors (different photoperiods and root temperature), *R* the region factor, *S* the seed source factor which is nested within factor region (*R*), and  $\varepsilon$  is the error term. Consequently, pairwise comparisons were conducted by Tukey's multiple comparison tests to determine specific differences among seed sources. A simple regressions analysis were carried out to look at the response of seed sources planted at different gardens as function of the climate of source locations (genecology) and as a function of the difference between source and planting site climate. Further regression analysis was done with response variables (JD and GDD) to predict the effect of seed transfer distance. Seed transfer distance was defined as the latitudinal difference of the seed origin and garden location (latitude of seed origin – latitude of garden location). The genecology relationship was done separately because interaction between regions and garden were significant (Table III).

## **Results**

### *Effect of location*

Variation in budburst phenology among the garden locations, climatic regions, and garden by climatic region interaction were significant ( $\alpha = 0.05$  and  $p < 0.001$ ) in both years (1998 and 1999) (Table III). Paper birch planted at the southern garden required fewer JD (range 72–92) to break bud compared to central (range 94–110) and northern (range 106–117) gardens (Figure 2). When the 18 populations were pooled and placed into five regional groups, seed sources from different regions were observed to respond differently at different gardens. The seed sources from the Kamloops (SC) region were first to break bud followed by Nelson (SE), Prince Rupert (NW), Cariboo (C), and Prince George (NC) regions in both years at all three

Table III. Analysis of variance (general linear model) results for 50% bud break in 1998 and 1999 by on Julian days and growing degree days (GDD).

	Sum-of-Squares	df	F-Ratio	p
Julian days year 1998	$R^2 = 0.849$ and $N = 932$			
Garden	89,550.311	2	2040.705	<0.001
Region	11,398.266	4	129.874	<0.001
Garden $\times$ Region	2448.599	8	13.950	<0.001
Source (region)	7621.463	13	26.720	<0.001
Error	19,834.682	904		
Julian days year 1999	$R^2 = 0.853$ and $N = 1153$			
Garden	120,875.642	2	2707.477	<0.001
Region	11,317.763	4	126.753	<0.001
Garden $\times$ Region	2400.728	8	13.443	<0.001
Source (region)	8684.725	13	29.927	<0.001
Error	25,112.880	1125		
GDD year 1998	$R^2 = 0.848$ and $N = 932$			
Garden	5,581,480.580	2	2053.626	<0.001
Region	664,624.988	4	122.270	<0.001
Garden $\times$ Region	162,521.924	8	14.949	<0.001
Source (region)	457,975.989	13	25.924	<0.001
Error	1,228,475.378	904		
GDD year 1999	$R^2 = 0.724$ and $N = 1153$			
Garden	2,246,982.595	2	935.501	<0.001
Region	645,700.777	4	134.414	<0.001
Garden $\times$ Region	122,646.515	8	12.766	<0.001
Source (region)	497,161.543	13	31.844	<0.001
Error	1,351,070.921	1125		

Note: Significant ( $\alpha = 0.05$ ) results are in bold and shaded.

garden locations except the southern garden where the Nelson region was first in 1998 and Cariboo was last in 1999 (Figure 3).

With respect to the heat (GDD with 0°C base) requirement for bud break of the 18 seed sources,

significant ( $\alpha = 0.05$  and  $p < 0.001$ ) effects were found among the gardens. Paper birch planted at the northern garden required the least heat followed by central and southern garden in both years (Figure 2). For different seed sources the heat requirement

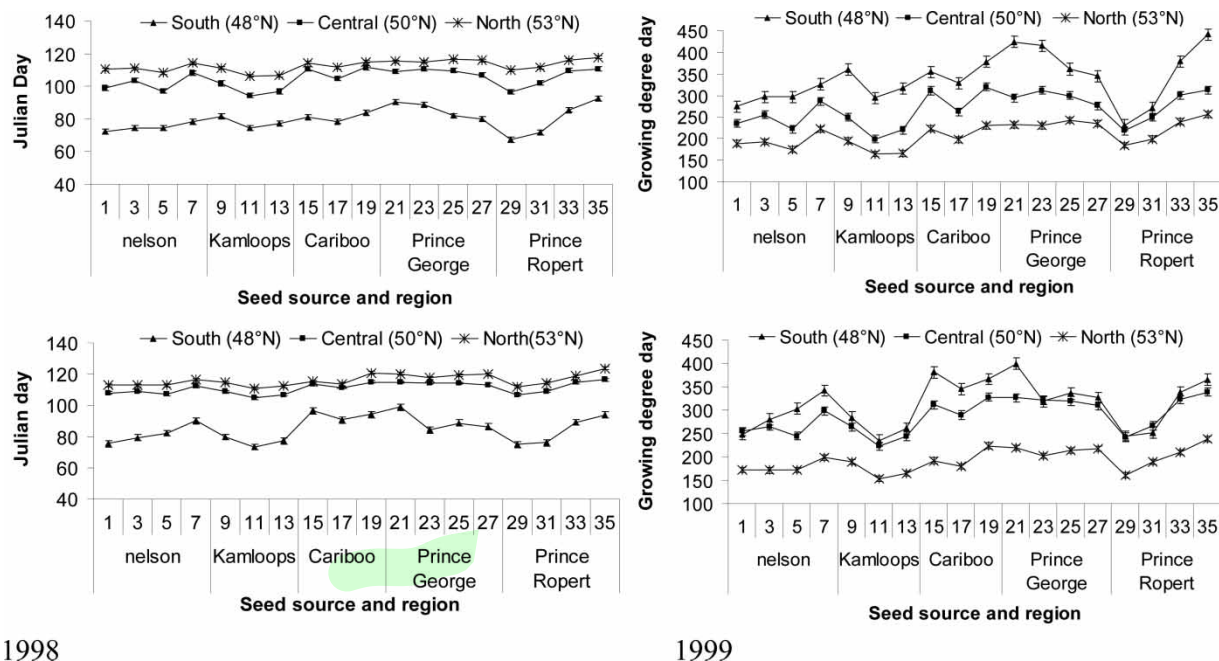


Figure 2. Fifty percent birch bud break ( $\pm$  SEM) of 18 seed sources by Julian day and growing degree day in 1998 and 1999.



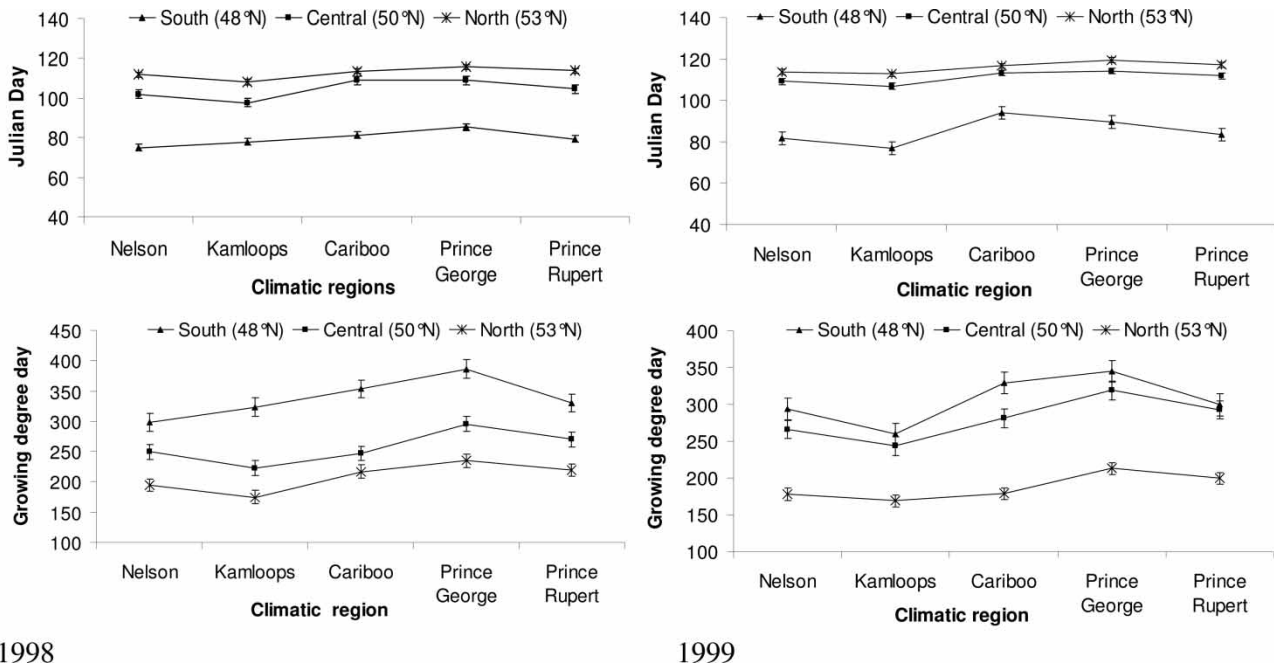


Figure 3. Fifty percent birch bud break ( $\pm$  SEM) by Julian day and growing degree day based on climatic regions in 1998 and 1999.

to bud break was quite well differentiated among the garden locations in both years (Figure 2). Based on seed sources from five climatic regions, a significant main effect on birch bud break was also found ( $p < 0.001$ ) in both years. Among the climatic regions, when Nelson seed source (southern population) is planted at the northern garden they require less heat (103 GDD or heat units) to break bud compared to when they are in the southern garden (Figure 3). While the Prince George seed source (northern populations) grown at the southern garden they require more heat (150 GDD) than the northern garden. This suggests for heat requirement, paper birch populations showed an inverse latitudinal trend. However, there was a significant ( $p < 0.001$ ) garden by region interactions and the stability of flushing order through three gardens suggests bud break is under genetic control. Based on nested (seed source nested within the Regions) ANOVA the JD and GDD demonstrated almost same proportion of total population variance and all effects were significant ( $\alpha = 0.05$  and  $p < 0.001$ ) in both years which also indicated the existence of genetic differences (Table III). Tukey's test for multiple comparisons ( $\alpha = 0.05$ ) revealed a significant difference among the most of climatic regions in both years based on JD and GDD. However, an insignificant difference between Prince George and Cariboo ( $p = 1.000$ ,  $p = 0.848$ ), Nelson and Prince Rupert ( $p = 0.437$ ,  $p = 0.105$ ), were observed in both years for JD requirement. While for GDD an insignificant difference was observed between Prince George and Cariboo ( $p = 1.000$ ,  $p = 0.335$ ) in 1999

and between Nelson and Prince Rupert ( $p = 0.987$ ) in 1998. This might be due to the close proximity of Prince George and Cariboo, the climatic difference between the years for Nelson and Prince Rupert.

Furthermore, when we did the regression analysis for JD to bud break and GDD with source location climatic variables, a poor relationship ( $R^2$ ) was observed and none of variable can explain more than 20% of variation (Table IV).

#### Effect of translocation experiment

For the translocation experiment from north to central garden, a significant garden effect ( $\alpha = 0.05$  and  $p < 0.001$ ) was observed. The samples translocated to the central garden flushed first (6.8–15.5 JD sooner than in the north) but required more heat (34–91.8 GDD) compared to those in the northern garden (Figure 4). The average JD required to bud flush for central and northern gardens were 113 and 123 whereas mean GDD were 275 and 208, respectively. When the 18 seed sources were pooled by climatic region, a significant difference ( $\alpha = 0.05$  and  $p < 0.001$ ) was observed among regions for both JD and GDD. When seed sources were nested within the Region, the effect was also significant. The Kamloops seed sources required the least JD and GDD in both garden locations whereas the highest JD and GDD were required for the Cariboo seed sources at the northern garden and Prince George seed sources at the central garden. When we compared the different regions with respect to garden location, the Cariboo seed sources showed



Table IV. Coefficient of determination ( $R^2$ ) of the linear regressions to 50% bud break based on origin of different seed source's environmental variables and seed transfer distance at the three garden locations in 1999.

Garden	Response variable	FFP	MAT	DD > 5	PPT	Latitudinal difference
South (48°N)	Julian day	0.19	0.23	0.21	0.08	0.070
	GDD	0.19	0.22	0.20	0.07	0.073
Central (50°N)	Julian day	0.09	0.19	0.20	0.02	0.150
	GDD	0.10	0.20	0.21	0.02	0.165
North (53°N)	Julian day	0.06	0.13	0.15	0.008	0.191
	GDD	0.06	0.14	0.17	0.007	0.198

MAT, mean annual temperature; DD > 5, degree days above 5°C; FFP, frost free period; PPT, Precipitation; GDD, Growing degree day.

the greatest difference among regions and they required 12 fewer JD at central garden than those planted at the northern garden. However, the greatest heat units (80 GDD) were required for Prince George populations at the central garden than the northern garden (Figure 4).

#### Effect of photoperiod

Analysis of variance results from the controlled environment experiment showed that photoperiod had a significant ( $\alpha = 0.05$ ,  $p < 0.001$ ) effect on bud break in the January experiment whereas in February the trend was still apparent but it was not significant ( $p = 0.07$ ) (Table V). This might indicate that with the increasing of time the amount of chilling is increases, which decreases the regulatory role of photoperiod in birch bud break. When the 10 populations were pooled into the five climatic regions, a significant difference was observed among the regions in both experiments (Table V). The photoperiodic response in bud burst is small, therefore it is difficult to determine a quantitative

contribution associated with it (Figure 5). Conversely, an insignificant photoperiod-region interaction in both years indicated that the response to photoperiod was not dependent on seed source region (Table V). Moreover, an ANOVA based on different test date (8 January and 20 February) indicated a significant testing date effect ( $< 0.001$ ) on bud break.

#### Effect of root temperature

Analysis of variance results indicated that cold and warm root temperatures significantly ( $\alpha = 0.05$  and  $p < 0.001$ ) affected budburst of birch and the cold root ( $0.8 \pm 0.7^\circ\text{C}$ ) treatment required more time (JD) to break bud compared to the warm root ( $13.8 \pm 1.2^\circ\text{C}$ ) treatment for all 10 seed sources (Figure 6). When we pooled seed source to climatic region there was also a significant ( $\alpha = 0.05$  and  $p < 0.001$ ) main effect of root zone temperature on bud break. Among the regions, seed sources from the Cariboo (15 days) showed the greater difference between cold and warm root treatments while the

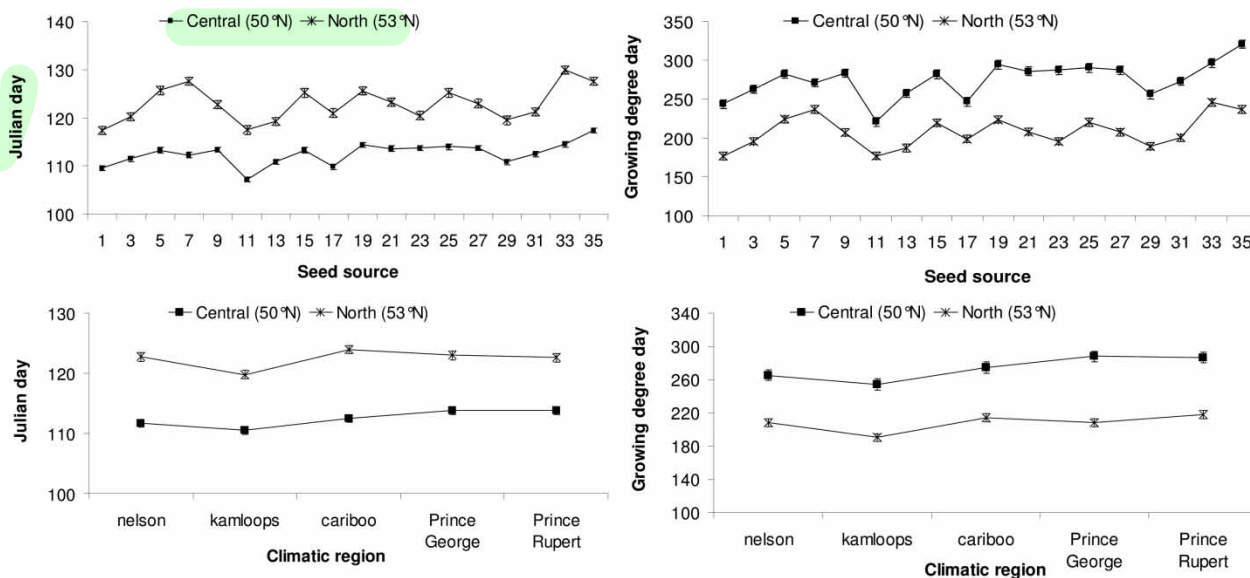


Figure 4. Fifty percent bud break ( $\pm$  SEM) by Julian day and growing degree day for the translocation experiment based on climatic regions and 18 birch seed sources.

Table V. Analysis of variance (general linear model) results for days to 50% bud break by short and long photoperiod treatments as well as different test dates (January and February).

	Sum-of-Squares	df	F-Ratio	p
January	$R^2 = 0.537$ and $N = 87$			
Photoperiod	60.656	1	18.035	<0.001
Region	98.178	4	7.298	<0.001
Photoperiod $\times$ Region	13.340	4	0.992	0.418
Sources (region)	111.539	5	6.633	<0.001
Error	242.147	72		
February	$R^2 = 0.459$ and $N = 92$			
Photoperiod	12.620	1	3.367	0.07
Region	99.623	4	6.644	<0.001
Photoperiod $\times$ Region	2.485	4	0.166	0.955
Sources (region)	127.402	5	6.797	<0.001
Error	288.640	77		
Different test date	$R^2 = 0.98$ and $N = 179$			
Testing date	60,142.877	1	14,732.652	<0.001
Region	165.822	4	10.155	<0.001
Test date $\times$ Region	27.663	4	1.694	0.154
Sources (region)	196.831	5	9.643	<0.001
Error	669.495	164		

Note: Significant ( $\alpha = 0.05$ ) results are in bold and shaded.

least difference was observed for the Prince Rupert region (6 days) (Figure 6). However, a significant ( $p = 0.027$ ) interaction of treatment by region indicated that the influence of root zone temperature during bud burst also depended on region: northern populations environmentally and genetically likely are habituated to colder root zone temperatures than the southern populations.

#### Effects of seed transfer distance

A linear relationship was observed between the birch bud break (JD) and latitudinal seed transfer distance ( $p < 0.001$ ) (Figure 7). The advancement of bud break was observed with decreasing the seed transfer distance toward south at the southern common garden whereas at northern garden it showed opposite trend. This indicates when seed sources moved from north to south require less time (JD) to bud break.

#### Discussion

Based on the different common garden results, seed sources in the southern garden required fewer JD to break bud compared to the central and northern gardens thus indicating that bud break is progressing from south to north (Figures 2 and 3). A similar result was observed by Balliet (2009) in another birch provenance study in BC and reported that birch bud flush follows the general geographic trend progressing from south to north. In another study O'Driscoll (1976) reported that the general geographic trend regarding bud break is progresses from south to north in Sitka spruce (*Picea sitchensis*). When we consider the mean date of the last spring frost occurrence at the three common garden locations, this also indicates a south to north trend (northern garden = 31 May; central garden = 7 May, and southern garden = 19 April) (<http://genetics.forestry.ubc.ca/cfgc/ClimateBC>). According to Ager et al. (1993), for bud break, timing of spring frost

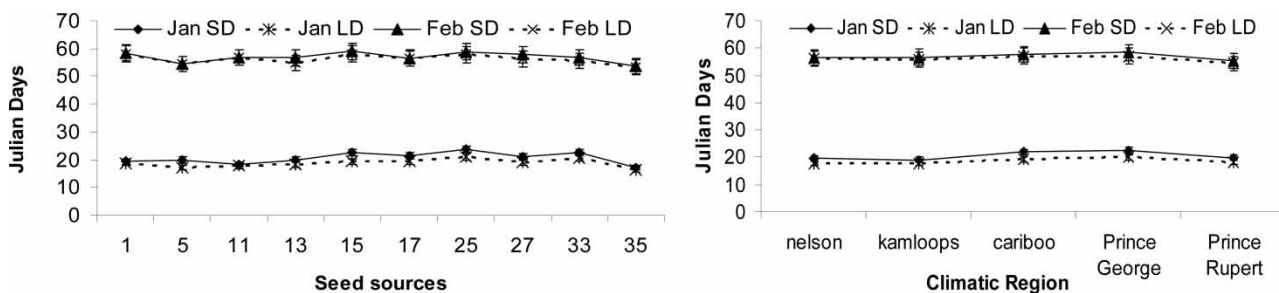


Figure 5. Julian days to 50% bud break ( $\pm$  SEM) in two photoperiods (Short day = 8 h and Long day = 16 h) based on climatic regions and birch seed sources.

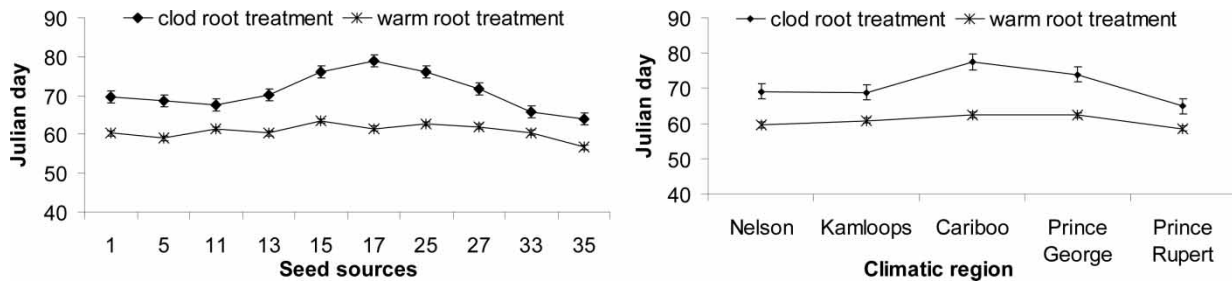


Figure 6. Effect of cold and warm root treatments on 50% bud break ( $\pm$  SEM) by Julian days.

may also play an important role and coincide with the mean date of the last damaging spring frost. However, in common garden studies it is evident that after latitudinal transfer the observed bud break is a consequence of an interaction between local ambient temperature and photoperiod (Li et al., 2003). Moreover, when we consider the mean April, May, and June temperature in 1998 and 1999 at the three garden locations (south = 12.1°C; central = 10.4°C; north = 9.6°C) the order of bud break revealed that temperature has an important role in birch bud break. Given this circumstance, it can be considered that if a transfer south is associated with warmer temperature then bud break will be quicker and if a transfer north is associated with colder temperature bud break should take longer. Other studies also reported that spring temperature is the most significant factor regulating the timing of vegetative budburst in plants (Linkosalo et al., 2006; Pudas et al., 2008; Veen, 1954; Wielgolaski, 2001).

For a given temperature, photoperiod at the northern garden is longer than at central and southern gardens (when mean air temperature is 10°C, photoperiod north to south garden is 17.5 h, 16 h, and 15.5 h, respectively) and this may influence the amount of heat (GDD) required for bud flush to initiate. According to Pudas et al. (2008) in early spring, photoperiodic constraints at lower latitude may have an influence on the requirement for higher GDD. Therefore, seed sources at the southern garden likely require greater heat accumulation than the central and northern gardens (Figure 3). Our translocation experiment also showed a similar result. When northern garden populations were translocated to the central garden the number of GDD (thermal) required for bud break increased an average of 66 GDD (Figure 4). Other studies also reported that plants grown at northern latitudes (LD) typically need less heat to flush than when the same population is grown at southern latitudes (SD) (Farmer, 1993; Heide, 1993; Pudas et al., 2008; Simpson et al., 2000). Another reason why the southern garden requires more GDD might be due to the amount of chilling received compared to the

northern garden location. According to Myking and Heide (1995), the chilling requirement increases with decreasing latitude due to the longer growing season. Based on a study of Norway spruce Hannertz et al. (2003) reported that northern provenances have lower chilling requirements than southern ones. In birch, however, the chilling requirement is relatively low and the expected effect of increased winter temperatures is earlier breaking of dormancy (Myking & Heide, 1995). This suggests that the amount of chilling may not be the cause for a higher GDD requirement at the southern garden. Moreover, our result also suggest that when southern populations were grown in the northern garden, they required less heat compared to their home condition or even less than the local populations (Figure 3). This might be the result of longer day-length in the early spring which reduced the heat requirement for bud break. According to Partanen et al. (1998), longer day-length is known to have a positive influence on spring bud development in Norway spruce (*P. abies*). Therefore, when southern populations are moved to the northern garden they are exposed to longer photoperiods and bud break begins with less heat (GDD) than in the south.

Although air temperature appears to be the most significant environmental factor influencing the initiation of bud burst (Hanninen, 1991; Kramer, 1995; Rohrig, 1991), photoperiod and soil temperature may also play an important role. Because temperature can vary significantly from year to year, particularly in the early spring, many temperate and boreal plant species also rely on photoperiod to constrain their development to "safe periods" (Häkkinen et al., 1998; Myking & Heide, 1995). The significance of this photoperiodic constraint appears to increase with increasing latitude of origin (Matyas, 1996; Morrison & Morecroft, 2006). Our controlled photoperiod experiment and seed sources translocation experiment both demonstrated that photoperiod had an effect on the initiation of bud break when they were equally chilled (Figures 4 and 5). In a recent study involving silver birch, Linkosalo and Lechowicz (2006) reported that simply meeting

chilling requirements is an insufficient signal for the initiation of bud development which occurs in silver birch around the spring equinox, months after chilling requirements have been met. This suggests that photoperiod plays an important role in the initiation of bud development in silver birch in the spring. Although some other studies reported that photoperiod does not influence growth onset if full chilling requirements have been met (Hänninen, 1990) or has no role in spring bud break (Leinenen & Kramer, 2002). Still others have suggested that the impact of photoperiod is species specific (Scharber & Badeck, 2003) or even specific to populations within a species (Irgens-Moller, 1957).

From our controlled soil temperature study, it was revealed that cold root treatments ( $0.8 \pm 0.7^\circ\text{C}$ ) delayed bud break compared to the warm root treatment ( $13.8 \pm 1.2^\circ\text{C}$ ) under the same 15 hour photoperiod and air temperature (Figure 6). These findings may also be supported by our common garden study. According to Balliet (2009) soil temperature of the northern garden would likely remain very close to freezing throughout the early growing season whereas in the central garden locations soil temperature should always remain above  $0^\circ\text{C}$  during the same time period. A similar trend has been also reported for a northern European *Betula* species' budburst study Wielgolaski (2001). In Ontario, Fraser (1956) reported that low air and soil temperatures were primary contributory factors delaying paper birch budburst in field studies near Chalk River. In another study, Aphalo et al. (2006) reported that growth depression of aboveground parts in response to low soil temperature was more significant in silver birch than other conifers. Thus it can be concluded that air temperature, photoperiod,

root zone temperature of the tree and their complex interaction(s) play an important role in regulating paper birch bud break.

When seed sources of continental or inland origin (Prince George) were compared with those of maritime or coastal origin (Prince Rupert), the order of bud flush followed an inverse longitudinal or continentality trend: that is, continental Prince George populations burst bud after maritime populations (Figure 3). This might be due to the combined maritime and continental climatic effect (Veen, 1954) because the local climate in Prince George is primarily continental but there is a maritime influence. A similar trend was observed by Gould et al. (2011) in Douglas-fir (*Pseudotsuga menziesii*), their model projection showed that coastal populations flush before continental populations.

The coefficients of determination for seed transfer distance in relation to JD and GDD were very low that is the unexplained variation was high (Table IV). This indicates that factors other than latitude must be involved in explaining the variation among the seed origins. However, this study reveals that northward seed transfers up to  $4^\circ\text{N}$  and southward up to  $7^\circ\text{N}$  should not be a problem as it only leading to later bud break than local sources (Figure 7). When southern populations are moved north or coastal population are moved inland (continental) there might be a chance of frost damage because frost resistance is generally lowest at bud break (Hannerz, 1994a) and the mean date of the last spring frost occurrence at the northern garden was later than at the southern garden (i.e. northern garden = 31 May; central garden = 7 May, and southern garden = 19 April). It is mentionable that beside the threshold temperature frost injury depends on some other

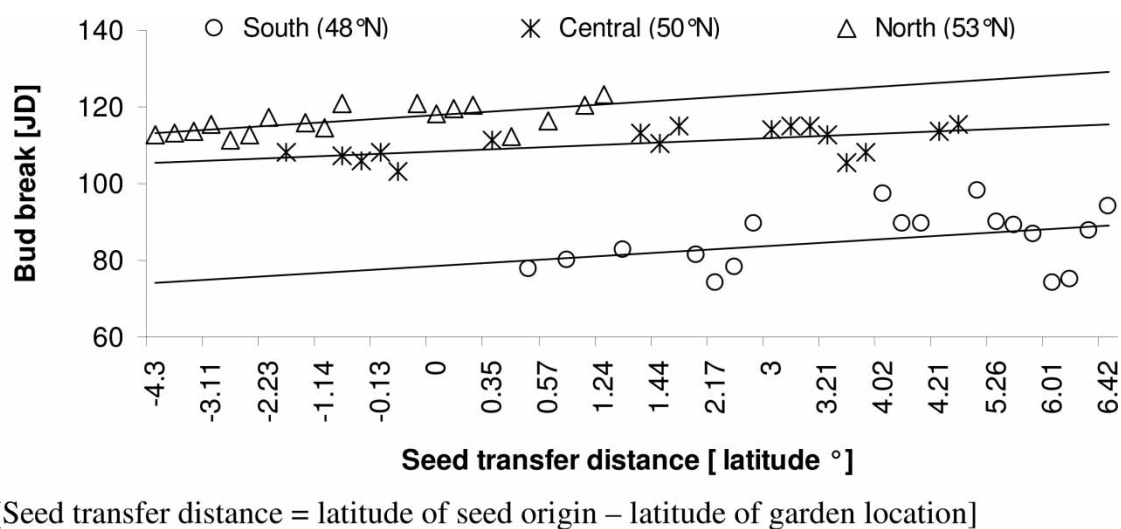


Figure 7. Julian days to 50% bud break of seed sources origin in relation to latitudinal seed transfer distance for the north (upper), central (middle) and south gardens (lower line).

factors such as seasonal variation of frost resistance, duration of low temperature, exposure to sun (Hannerz, 1994b)

## Conclusion

Results from this study suggest the onset of bud break in paper birch populations generally follows a latitudinal cline from south to north with air temperature, photoperiod and soil temperature of the location playing important roles. However considering heat (GDD), southern populations grown in the northern garden required less heat compared to their home condition or even less than the local (northern) populations to flush. In a controlled environment photoperiod and translocation experiments, photoperiod played an important role in the timing of birch bud break. Based on the two years data, the stability of flushing order (little annual variation) throughout the three gardens location as well as significant differences ( $p < 0.001$ ) among region and seed source nested within the region for garden. The translocation, photoperiod, and root temperature experiments suggest that birch bud break is under strong genetic control. However, differences in the number of days to and the amount of heat required for bud flush to occur at the different gardens indicates the environmental component also plays a substantial regulatory role. Moreover, birch seed sources transfer direction can be extended  $\leq 4^\circ$  latitude northward while  $\leq 7^\circ$  latitude in southward. All this information will be useful when developing seed zones and seed transfer guidelines for paper birch in BC. It will also aid in the investigation of the potential impacts of climate change on a selective birch breeding program.

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