Plant, Cell & Environment

Plant, Cell and Environment (2013) **36**, 116–127 doi: 10.1111/j.1365-3040.2012.02560.x

Timing of photoperiodic competency causes phenological mismatch in balsam poplar (*Populus balsamifera* L.)

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ABSTRACT

Plant phenology is expected to be sensitive to climate warming. In boreal trees, spring flush is primarily temperature driven, whereas height growth cessation and autumn leaf senescence are predominantly controlled by photoperiod. Cuttings of 525 genotypes from the full range of balsam poplar were planted into two common gardens (Vancouver and Indian Head, Canada) at similar latitudes, but with differing winter temperatures and growing seasons. There was clinal variation in spring and, particularly, summer and fall phenology. Bud flush and, despite milder climate, bud set and leaf drop were earlier at Vancouver than at Indian Head by 44, 28 and 7 d, respectively. Although newly flushed growth is insensitive to photoperiod, many genotypes at both sites became competent before the summer solstice. At Vancouver, high-latitude genotypes set dormant terminal buds in mid-spring. Most other genotypes grew until midsummer or set bud temporarily and then experienced a second flush. In both gardens and in a growth chamber experiment, earlier bud set was associated with reduced height growth and higher root/shoot ratios. Shoots attained competency ~5 weeks after flushing, which would normally prevent dormancy induction before the solstice, but may be insufficient if spring advances by more than a few weeks.

Key-words: bud flush; bud set; climate change; growing season length; height growth cessation; latitude; phenology; photoperiod.

INTRODUCTION

Trees from distinct climates adapt to their local environment by synchronizing their phenological processes to the changing seasons (Leith 1974; Cleland *et al*. 2007). North temperate and boreal hardwoods typically use the length of night as the primary environmental cue to time summer and fall phenophases such as height growth cessation (HGC), bud set, leaf senescence and leaf drop (Fracheboud *et al*. 2009). These photoperiodic responses have been under differential selection by the timing of the onset of cold temperatures (Bradshaw & Holzapfel 2001). A strong clinal gradient in the timing of summer and fall phenophases, which is correlated with the length of the growing period, therefore exists with latitude and altitude. The critical photoperiod (the day length corresponding to the threshold night length that triggers a phenological shift) increases with latitude and altitude as the length of the available growing season decreases. Timing of spring phenophases (such as flowering, bud burst, leaf unfolding and greening) on the other hand, while also synchronized with the native environment, is largely a function of temperature in most temperate and boreal trees. A chilling requirement (prolonged exposure to near-freezing temperatures) must first be met to break dormancy before buds can subsequently flush in response to a particular heat sum (temperature accumulated above a certain threshold; Kozlowski & Pallardy 2002; Howe *et al*. 2003). Clinal gradients in chilling requirements and possibly heat sums as well, also exist (Worrall 1983). Similar gradients in the timing of phenophases are also seen in other organisms (e.g. arthropods, birds, amphibians) with large latitudinal and altitudinal distributions (Bradshaw & Holzapfel 2008).

Climate change impacts on plant phenology have attracted much attention (e.g. Walther *et al*. 2002), partly because of the consequent effects on population and species distributions, species interactions and ecosystem productivity. Phenological processes are easily observable and are perhaps the most sensitive traits to climate change. It is recognized that the available growing season has increased at higher latitudes over the last several decades because of earlier onset of spring (Post *et al*. 2009) and later termination of autumn (Myneni *et al*. 1997). For trees to fully utilize the increasing growing season and compete effectively, an earlier growth initiation and later growth cessation and leaf senescence would be necessary. Flowering, bud burst and leaf unfolding are indeed occurring earlier (Menzel *et al*. 2006; Peñuelas, Rutishauser & Filella 2009). Although there is also evidence that warm temperatures extend the green-cover period (GCP) into the fall in temperate trees (Jeong *et al*. 2011), boreal species seem more conservative (Körner & Basler 2010). For example, the timing of leaf senescence in aspen in both Canada and

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Scandinavia is insensitive to annual temperature fluctuations (Barr *et al*. 2004; Pudas *et al*. 2008; Fracheboud *et al*. 2009). A rigid response to photoperiod for plants that occupy regions of severely cold winters is an insurance against unpredictable early frost events (Kramer 1936; Withrow 1959).

To fully understand the impacts of climate warming on growth and productivity of boreal or temperate trees, it is necessary to observe the complete growth phenology from bud burst to leaf senescence. The vast majority of studies have looked at spring phenology only, whereas the few (and more recent) studies looking at later phenophases concentrate on leaf senescence. It is often erroneously assumed that height growth cessation (HGC) and autumn leaf colouring are tightly correlated, and thus HGC and bud set are rarely monitored. However, Fracheboud *et al*. (2009) have shown that although HGC must precede leaf senescence, these are separate, independently cued events. A shift in the timing of HGC does not necessarily imply a shift in the timing of leaf senescence. Furthermore, HGC is a partially reversible process, whereas leaf senescence seems not to be. For example, abiotic stress such as drought and heat can induce HGC followed by bud formation even under long days. If conditions improve, however, and before the terminal buds are fully formed and dormant, they may undergo a second flush and begin growth again. Such 'lammas' shoots are distinct from proleptic and sylleptic shoots that arise from newly formed lateral buds or directly from leaf axils, while height growth is still active (Kozlowski & Pallardy 1997).

Rates of species migration and/or gene flow in forest trees will likely be too slow to keep pace with expected 21st century climate change – therefore, substantial adaptational lag is expected (Aitken *et al*. 2008). High-latitude boreal habitats are expected to experience particularly extreme shifts in temperature (IPCC 2007). Although temperature shows considerable year-to-year variation, photoperiodic regime is completely predictable and depends only on latitude and time of year. It will, of course, remain static with climate warming. Natural and/or assisted migration to higher latitudes will cause populations to experience photoperiods different from what they are currently adapted to (Howe *et al*. 2003); likewise, extant populations may become maladapted to local photoperiodic regime because of changes in growing season length.

Here, we report results from 3-year observations of spring, summer and fall phenophases and the resultant biomass production in a range-wide collection of balsam poplar (*Populus balsamifera* L., *Salicaceae*) planted into two common gardens with similar photoperiods, but with differing mean winter temperatures and growing season lengths. Balsam poplar is a dominant north temperate to boreal hardwood species with an extensive distribution in North America (Fig. 1), with mean annual temperatures and maximum day lengths ranging from –8.8 to 10 °C and 15.3 to 24 h, respectively. Our hypothesis was that under

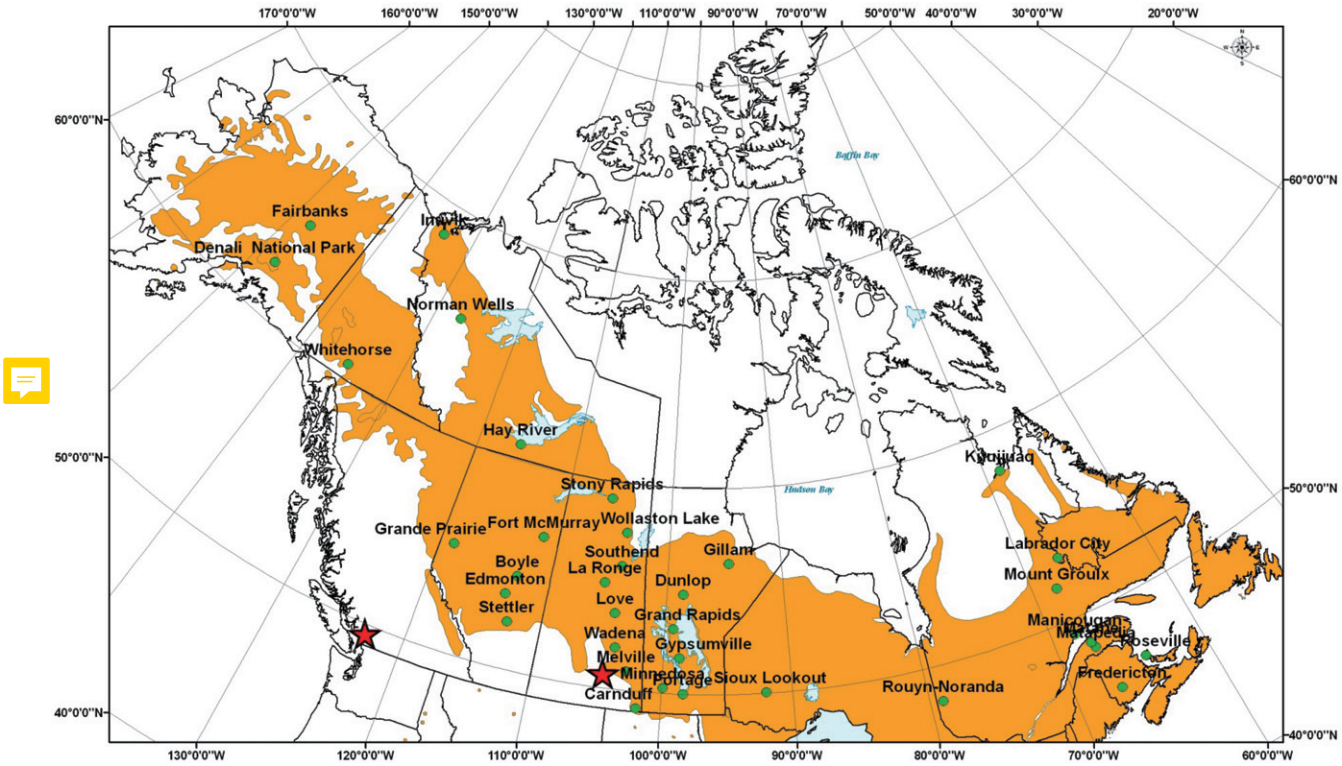

Figure 1. Natural range of *Populus balsamifera* (colour shaded area) and the geographic origins of 35 provenances planted in two common gardens (Vancouver and Indian Head, marked by stars).

warmer climatic conditions, high-latitude or near-arctic genotypes would be particularly prone to phenological mismatch because they are adapted to regions with rapid annual progressions in photoperiod that cue their development over a very tight season (as little as 3 months, from bud burst to leaf drop). We asked (1) to what extent are phenophases in balsam poplar populations plastic to climate warming?; (2) are spring, summer and fall phenological events plastic to the same extent, in the same direction?; and (3) if not, what is the impact of this uncoupling on biomass productivity and partitioning? We highlight how photoperiodically cued, but temperature selected, phenophases may influence adaptation to climate warming. In addition, we elucidate a role for photoperiodic competency, the age-dependent ability of vegetative shoots to cease height growth in response to their critical photoperiod. This neglected physiological phenomenon may have a major impact on the timing of subsequent events when spring growth starts early.

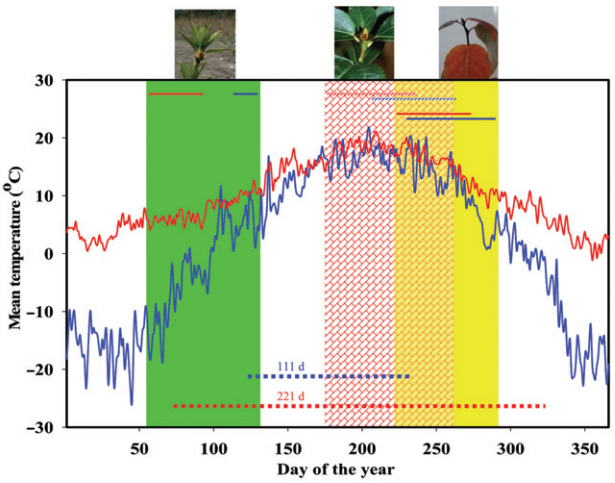

Figure 2. Balsam poplar phenological events plotted with mean temperature for both common gardens. The red colour line denotes Vancouver while the blue is the Indian Head common garden. The dashed lines at the bottom indicate the numbers of frost-free days available for growth at Vancouver and Indian Head. The green band denotes the period over which spring events occur, while brown hatching denotes bud set and yellow indicates leaf senescence. The lines near the top of the panels indicate these periods at each common garden.

MATERIALS AND METHODS

Genetic material and common garden sites

The genetic material used in this study is a subset of a larger Agriculture Canada Balsam Poplar (AgCanBaP) collection representing 65 provenances composed of 15 distinct trees (genotypes) sampled per provenance (Fig. 1). For more information on sampling procedure refer to Soolanayakanahally *et al.* (2009). Details regarding the origins of the 35 populations used in this study are given in Supporting Table S1 (see also Fig. 1).

This study makes use of two common gardens: one at Vancouver, British Columbia (49.26°N 123.25°W; elevation 82 m) and the other near Indian Head, Saskatchewan (50.52°N 103.68°W; elevation 605 m), Canada. Mean annual temperature based on 1961–1990 climate data is 9.7 and 2.0 °C, respectively (Wang *et al.* 2012). Average growing season is 110 d longer in Vancouver than in Indian Head (Fig. 2). Maximum day length, on the other hand, is very similar (16 h 15 min and 16 h 28 min, respectively). Both gardens were equipped with weather stations. Over the 3 years of this study, mean maximum summer temperature was 20.5 °C and 21.8 °C and mean annual precipitation was 1277 mm and 447 mm, respectively, at Vancouver and Indian Head. The AgCanBap collection has since been established in common gardens at three other locations not used in this study.

Common garden establishment

From each genotype, dormant whips of 6–9 cm with a minimum of two buds were forced to root in Spencer-Lemaire rootrainers (Beaver Plastics, Acheson, Canada) filled with a mixture of Sunshine-2 (Sun Gro Horticulture, Vancouver, Canada) growing mix (60%), peat moss (30%) and vermiculite (10%). The rooted cuttings were grown in a greenhouse during the spring of 2006 with natural light supplemented with artificial lighting by cool-white fluorescent lamps to provide a 21 h photoperiod and a minimum fluence of 400 μmol m^{-2} s^{-1} PPFD at plant level. Maximum day and night temperatures were maintained close to 25 and 18 °C, respectively. Upon flushing, the plants were well watered and fertilized with Hoagland's solution (Hoagland & Arnon 1950). In early June, when all plants were approximately 30 cm tall, they were moved to a shade house. The Vancouver common garden was planted in June 2006 and the one at Indian Head was planted before bud flush in May 2007. Because both sets of plants completed growth outdoors in their first year (2006), they were of comparable size across the two common gardens when phenology scoring began in early 2007. Fifteen genotypes from each provenance were planted in a group at 2 m × 2 m spacing and groups (provenances) were then randomized within blocks (i.e. two ramets per genotype at Vancouver and five ramets per genotype at Indian Head). The Vancouver common garden was sprinkler irrigated as necessary during the summer months. Irrigation was not necessary at Indian Head in the years under study.

Phenological observations

Spring and autumn phenology characterized by bud burst and bud set were monitored for three seasons (2007, 2008 and 2009) in the two common gardens. Leaf senescence was only scored in 2009. At each site, the observations were recorded by the same personnel walking through the common garden twice a week (every Tuesday and Friday). A scale of 0 to 10 was used to describe the different

phenological stages. During early spring, the developmental stage of the terminal buds of each tree was scored on a scale from 0 to 3 (0 = dormant bud, 1 = bud swollen, 2 = bud open with visible green tip, 3 = complete bud flush). This was immediately followed by recording leaf unfolding (very small leaves with visible petiole, stage 4).

Within a few weeks of leaf unfolding, we began scoring the condition of the apical meristem of the current-year terminal shoot on a scale from 5 to 7 (5 = current terminal of the main stem actively growing, 6 = terminal bud beginning to form on shoot apex, 7 = final bud set with terminal bud fully developed and covered by dark brown scales). In 2008, we also recorded lammas growth when it occurred, which is defined as a secondary flush from a newly formed bud before entering stage 7. In these cases, the second bud set was taken as the final bud set. Leaf senescence dates in autumn were recorded as stages 8 to 10, using the Swedish aspen senescence score card (Fracheboud *et al*. 2009), whereby 8 = ~25% of the leaves on the tree turned yellow, 9 = ~50% of the leaves on the tree turned yellow and 10 = 100% leaf drop. The tree-averaged GCP was calculated as the difference between the day of the year (DOY) recorded for stages 4 and 9.

Height measurements and root:shoot (R:S) ratio determination

End-of-season tree heights were measured at the Indian Head common garden in fall 2008. To better assess total plant growth and to estimate the R:S ratio, we harvested three to seven trees from seven populations representing two latitudinal transects (see Supporting Information Table S1) in both common gardens before bud flush during the spring of 2009. The excavated roots and complete aboveground shoot of each tree were collected separately in brown paper bags and stored in cooler boxes for transfer to the laboratory. Most of the fine roots (<1 mm diameter) were not recovered but enough care was taken to get close to 85–90% of the remaining roots from each tree. In the laboratory, roots were separated from the soil by washing manually under running tap water on a sieve (1 mm mesh). Roots and shoots were oven dried at 70 °C to constant mass for computation of the R:S ratio.

Growth chamber experiment

To estimate the length of time needed for new growth to reach photoperiodic competency and then cease height growth in response to a change in photoperiod, we conducted a growth chamber experiment. A subset of four genotypes from six populations (Minnedosa, Love, Fort McMurray, Hay River, Kuujjuaq and Norman Wells; see Supporting Information Table S1) covering a range of latitude from 46.40°N to 65.23°N were rooted as above in 965 mL Ray Leach Deepots D20 cells (Stuewe & Sons, Tangent, OR, USA) and grown in two growth chambers having different photoperiods (20 and 16 h). The temperature regime was the same in both chambers; day/night 20 °C. Beginning 4 weeks after flushing (stage 3) under long photoperiod (20 h), one ramet from each of the four genotypes per population was moved to the short photoperiod (16 h) chamber at regular intervals. Controls from each population were also grown under both photoperiods. Height increments were recorded every second day throughout the experiment, and date of bud set (stage 7) was recorded. The experiment was terminated after 80 d growth when plants were harvested for determination of R:S ratio as above.

Statistical analysis

All statistical analyses used SAS version 9.1.3 (SAS 2002/2003) or SigmaPlot 11.0 (Systat Software, San Jose, CA, USA). One- and two-way analysis of variance (ANOVA) was performed to test for effects of provenance and/or differences between common garden sites. Where possible, data were transformed to conform to assumptions of normality and homogeneity of variance; otherwise, ANOVAS on rank were performed. Regression lines in figures are based on population means within each common garden. Common garden averages for each phenological event were calculated from pooled data across years.

RESULTS

Balsam poplar phenology

Large differences in timing of spring phenophases and smaller differences in summer and fall phenophases were observed between the two locations (Table 1). Spring is earlier and less abrupt in oceanic as compared to continental climates. The average date of bud flush (stage 3) was 44 d earlier at the Vancouver common garden compared to the Indian Head common garden ($P < 0.001$; Fig. 3a). There was also a significant garden × latitude interaction effect ($P < 0.001$), whereby bud flush occurred over a longer period at Vancouver as compared to Indian Head (29 versus 17 d, respectively), reflecting the differences in speed of temperature increase between the two locations at the different times. Bud flush date and latitude of origin were negatively correlated (Vancouver: $r = –0.692$, $P < 0.001$; Indian Head: $r = –0.517$, $P = 0.001$) but the slope of this relationship was not steep at either location.

After photoperiodic induction, it takes a few days for height growth to cease and about 4 weeks for buds to set a resting bud (stage 7). The formation of a terminal bud therefore marks, with about 3 $^1/_2$ weeks delay, the end of height growth. The average date of final bud set took place 28 d earlier in Vancouver, despite more favourable late season temperatures, than in Indian Head ($P < 0.001$; Fig. 3b). Strong clinal variation in date of bud set with latitude of origin was seen at both locations (Vancouver: $r = –0.938$, $P < 0.001$; Indian Head: $r = –0.977$, $P < 0.001$). The higher the latitude of origin, the earlier the bud set.

Table 1. Three-year means (± SE) for phenological events (day of year, DOY) scored in both common gardens across all *Populus balsamifera* genotypes. Height growth duration, green-cover period (GCP) and absolute differences between sites are shown as number of days

Phenological event	Stage no.	Vancouver (49.26°N 123.25°W)	Indian Head (50.52°N 103.68°W)	Absolute difference between site means
Bud flush	3	79 ± 0.88	123 ± 0.75	44
Leaf unfolding	4	90 ± 0.88	132 ± 0.75	42
Final bud set	7	206 ± 4.31	234 ± 3.83	28
50% leaf yellowing	9	243 ± 1.76	259 ± 2.55	16
100% leaf drop	10	270 ± 2.54	277 ± 2.77	7
Height growth duration	7–4	116	102	14
GCP	9–4	153	127	26

Indeed, in Vancouver (the milder location), final bud set in most of the high-latitude populations (63.87°N to 68.38°N) occurred almost 2 $^1/_2$ weeks before the summer solstice (21 June), while day length was still increasing (Fig. 3b), and photoperiodic induction of height growth cessation would have been at least 4 weeks prior, in late April or early May. There was no clear garden × latitude interaction effect ($P = 0.07$). Although the relationship with latitude of origin was probably more curvilinear than linear at Vancouver as compared to Indian Head, the difference in date of final bud set between the most northerly (Inuvik, 68.38°N) and southerly (Fredericton, 46.40°N) populations was approximately 88 d at both locations. Populations had, on average, an additional 14 d for height growth (calculated based on the difference between stages 7 and 4) in Vancouver compared to Indian Head. This contrasts with the overall difference in growing season length of about 110 d between the two locations. The extra 14 d of realized growth in Vancouver relative to Indian Head might be expected, overall, to yield taller plants, but those days occur entirely under the near-limiting temperatures (Fig. 2) and low light levels of early March. Furthermore, for many genotypes, the period of active height growth was regularly interrupted in Vancouver.

The population means plotted in Fig. 3 obscure considerable within-population variation in bud phenology, particularly among the mid-latitude and some low-latitude populations growing in Vancouver. In addition to this variation, second flushing (lammas) occurred in many populations but in Vancouver only (Fig 4a). In these cases, renewed shoot growth continued for 3 to 12 weeks before a second and final bud set was recorded as stage 7. The frequency of second flushing was particularly high in mid-latitude populations (Fig 4b). With the exception of the most southerly population (Fredericton), the most common pattern for low-latitude genotypes was to grow continuously from bud break in spring until bud set in late summer or autumn. Although the high-latitude populations set bud much earlier, they did not lammas. Only one genotype out of 90 sourced from above 60°N had a second flush. Many genotypes from other populations, however, tended to have an initial bud set just before or not long after the solstice, but would then flush and grow until setting bud again later in the year. In sharp contrast to final bud set dates, there was a weak but significant reverse clinal pattern in date of lammas bud formation ($r = 0.265$, $P = 0.001$). In the majority of cases, buds that lammased were set prior to or near the solstice, but there seemed to be another wave of bud formation towards the end of July. In no case did an individual tree lammas more than once.

Even among the low and mid-latitude populations there were several genotypes that behaved like the northern populations by prematurely setting final buds (near the solstice) that did not lammas, resulting in a bimodal clustering of bud set dates (Supporting Information Fig. S1). For most of the remaining genotypes able to grow continuously through the solstice, the dates of bud set at Vancouver and at Indian Head were coincident. Likewise, within a population, final bud set occurred at about the same time regardless of lammas growth (not shown).

There was a strong clinal pattern for leaf senescence with latitude of origin (Fig. 3c, Vancouver: $r = –0.818$, $P < 0.001$; Indian Head: $r = –0.934$, $P < 0.001$). Unlike bud flush and bud set, however, leaf senescence was more coincident between the two common gardens, and there was also a strong garden × latitude interaction effect ($P < 0.001$). On average, stage 9 (50% yellowing) occurred just 16 d earlier in Vancouver than in Indian Head. The difference was greater for low-latitude populations than it was for the high-latitude populations, which had similar dates of leaf senescence in both gardens. Although stage 3 started earlier in Vancouver by ~44 d, complete leaf drop (stage 10) at both locations occurred more or less at the same time (Table 1).

The GCP (i.e. the period between stages 4 and 9) averaged 26 d longer in Vancouver than in Indian Head. In contrast, the average portion of the GCP occurring before bud set (stage 7) was 30 d shorter in Vancouver than in Indian Head, leaving 81 d remaining to reach stage 9 at Vancouver but just 25 d at Indian Head. Given data presented in Fig. 2, the pre- and post-bud set portions of the GCP must also vary with latitude of origin. These differences are expressed in Supporting Information Fig. S2 as a ratio of the number GCP days that occur after final bud set over the number of GCP days that occur before final bud set (GCP ratio). The GCP ratio increased several-fold with latitude of origin ($P < 0.001$), and was higher in Vancouver than in Indian Head ($P < 0.001$). There was a significant garden × latitude interaction effect ($P = 0.003$).

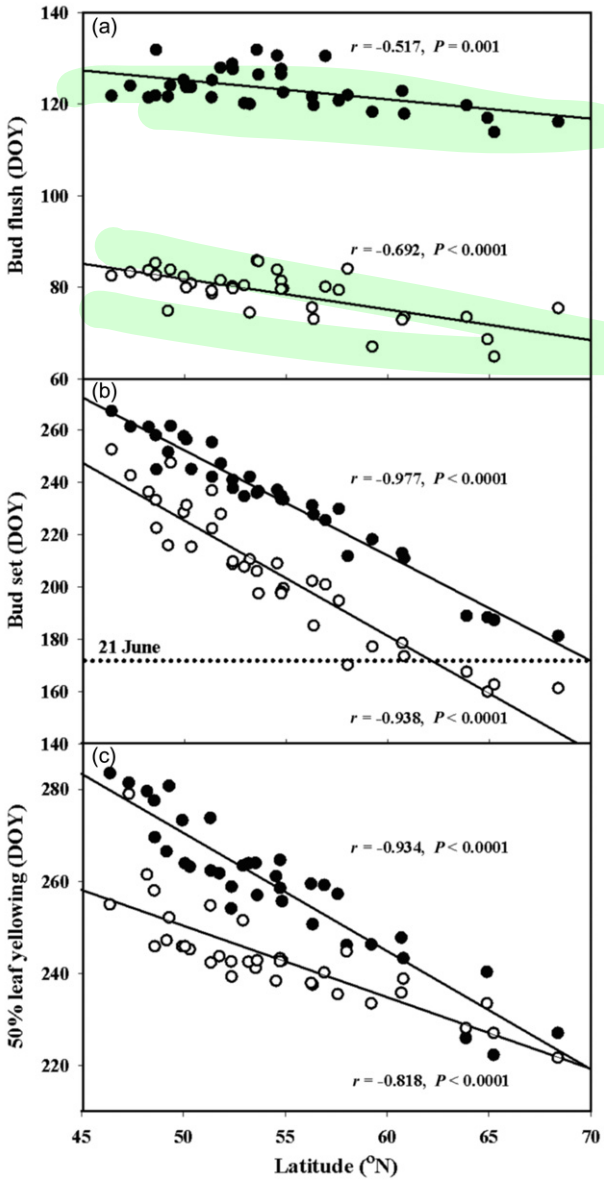

Figure 3. Latitudinal clines in phenology among 35 *Populus balsamifera* provenances for mean dates of (a) bud flush, (b) final bud set and (c) 50% leaf yellowing at Vancouver (open circles) and at Indian Head (closed circles) common gardens. The dotted line indicates the summer solstice (21 June). DOY, day of year; error bars omitted for clarity.

Height growth, biomass and R:S ratio

Population differences in date of bud set and, less so, leaf flush were reflected in differences in height growth. As shown for the Indian Head garden in Fig. 5, height after 2 years was strongly related to the seasonal duration of shoot extension. Because the shape of the bole approximates a cone, these differences in height translate into even greater differences in biomass (Table 2). There was a more than 10-fold variation in shoot dry mass at both common gardens. Population differences in root dry mass were much less dramatic but still very significant (threefold in Vancouver and almost sixfold in Indian Head; interaction significant at $P = 0.005$). Growth of all excavated genotypes was greater at Indian Head ($P < 0.001$) but because of the even greater clinal differences, there was population overlap across the gardens (e.g. total biomass of Fredericton planted at Vancouver still exceeded Kuujjuaq, Hay River and Norman Wells planted at Indian Head). Clinal variation in R:S ratio was clear at both gardens ($P < 0.001$); for example, at Indian Head, the R:S ratio for Norman Wells was 2.5× larger than for Fredericton, whereas at Vancouver it was 6.1× larger (Table 2). R:S ratios were higher across all but one population (Fredericton) in Vancouver than in Indian Head (interaction significant at $P = 0.055$). The overall mean R:S ratio at Vancouver was 2.12, whereas at Indian Head, it was 1.15 ($P < 0.001$). A combination of data from both locations shows that R:S ratio was linearly correlated with GCP ratio (Fig. 6).

Growth chamber experiment

Shoot cuttings rooted in the growth chamber flushed at approximately 7 d, typically yielding 5–8 pre-formed leaves.

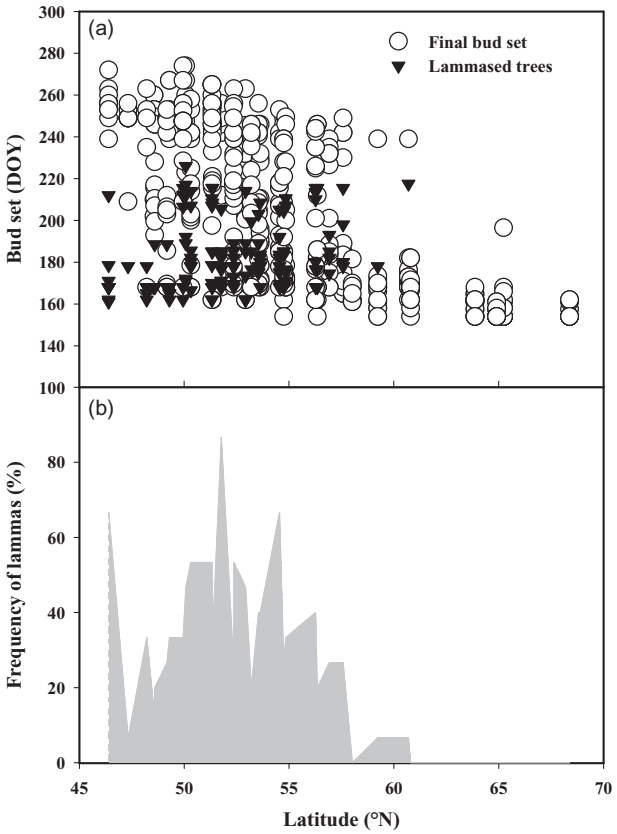

Figure 4. Bud set and lammas pattern within each provenance at Vancouver in 2008. (a) Bud set dates for all genotypes. Open circles indicate day of year (DOY) when final bud set occurred. Inverted triangles indicate the initial date of bud set in genotypes that had a second flush (lammas) followed by renewed shoot growth before final bud set was recorded. (b) Frequency of lammas growth among provenances.

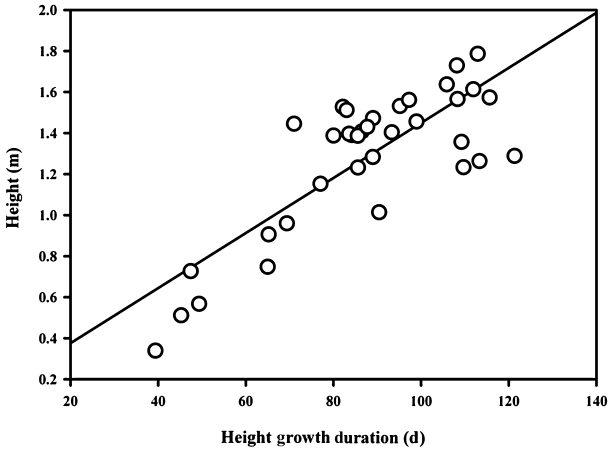

Figure 5. Mean heights of 35 *Populus balsamifera* provenances after 2 years growth at the Indian Head common garden. Data are plotted as a function of height growth duration, which is the number of days between bud flush (stage 3) and bud set (stage 7), less 24 d to account for the delay between height growth cessation and completion of bud development. Error bars omitted for clarity.

Afterwards, shoots continued to grow indeterminately and produced numerous neoformed leaves until HGC. The long-day treatment (20 h) was sufficiently long to maintain active growth in most but not all populations (e.g. Norman Wells). The short-day treatment was sufficiently short to induce growth cessation in most ramets from Norman Wells, Hay River, Kuujjuaq, Fort McMurray and Love, but not in Minnedosa. Data in Fig. 7a are only for ramets where a 16 h photoperiod was sufficient to induce HGC. On average, controls maintained at 16 h from the beginning of the experiment (i.e. 'transferred' at 0 d) ceased height growth 39 d after flushing. Likewise, plants transferred from one chamber to the other were not competent to respond to a reduced day length until reaching this age. Once plants became responsive to photoperiod, height growth ceased about 4 d after transfer, with prominent visible green buds (stage 6) formed about 15 d after transfer. The final R:S ratios of transfers to the 16 h chamber are shown in Fig. 7b. The highest mean R:S ratio (1.51 ± 0.17 SE) was in the 16 h control treatment. Later dates of transfer resulted in lower R:S ratios. Low R:S ratios (0.70 ± 0.12 SE) were also observed in plants remaining in the 20 h treatment (not shown), where height growth continued.

DISCUSSION

Bud phenology in an extended season

Extended growing season, evidenced by earlier occurrence of spring phenophases as a result of climate warming, is already occurring at higher latitudes (Stöckli & Vidale 2004; Piao *et al*. 2008; Morin *et al*. 2009; Post *et al*. 2009). The full impacts of this extended growing season on tree phenological processes and the impacts of these processes on tree growth, productivity and ecosystem C accumulation are only beginning to be understood (Barr *et al*. 2004, 2007). Here, we were interested in knowing the extent to which primarily photoperiod-driven phenological processes, such as growth cessation and leaf senescence, are affected by an extended season (earlier spring and a later autumn). We also wanted to know the impacts of shifts in phenological processes on tree growth and productivity. Results from our studies with range-wide *P. balsamifera* populations grown at two locations with similar photoperiod regimes but very different temperature regimes reveal a counterintuitive phenology-driven tree growth response to an extended growing period. As expected, the spring phenophases occurred earlier at the milder site, but so too did the summer and fall phenophases.

Bud flush and leaf unfolding (the beginning of the GCP) were advanced by approximately 44 d in balsam poplar trees at Vancouver compared to Indian Head. This is in accordance with an earlier spring (by ~1 $^1/_2$ months) in Vancouver. Bud set, and thus HGC, however, also occurred earlier at the Vancouver site, by an average of 28 d across all populations. Thus, the extended autumn growing season

Table 2. Biomass and root:shoot (R:S) ratios of *Populus balsamifera* provenances excavated from both common gardens before the spring of 2009 (listed in order of high to low latitude). The common garden averages are also presented. Numbers are means (± SE), where $n = 3$ for each provenance at Indian Head and $n = 7$ for each provenance at Vancouver except Fredericton where $n = 5$. ANOVA *P*-values are for differences between provenances within gardens

	Shoot dry mass (g)		Root dry mass (g)		Total biomass (g)		R:S ratio	
Provenance	Vancouver	Indian Head	Vancouver	Indian Head	Vancouver	Indian Head	Vancouver	Indian Head
Norman Wells	10.2 ± 1.3	26.6 ± 3.7	31.4 ± 5.4	48.8 ± 10.3	41.5 ± 6.1	75.3 ± 13.8	3.28 ± 0.49	1.80 ± 0.19
Hay River	22.4 ± 2.8	69.7 ± 4.7	47.6 ± 8.0	82.4 ± 12.1	70.0 ± 10.4	152.1 ± 16.6	2.10 ± 0.27	1.17 ± 0.10
Kuujjuaq	18.4 ± 2.2	61.9 ± 3.0	52.5 ± 8.6	81.7 ± 10.4	71.0 ± 8.9	143.6 ± 10.1	3.03 ± 0.62	1.33 ± 0.20
Fort McMurray	38.0 ± 6.0	207.0 ± 24.2	66.0 ± 11.1	203.6 ± 32.9	104.0 ± 16.6	410.6 ± 55.6	1.80 ± 0.22	0.98 ± 0.07
Love	34.8 ± 9.5	148.2 ± 16.9	57.6 ± 9.9	155.2 ± 30.0	92.4 ± 19.2	303.4 ± 45.4	1.86 ± 0.18	1.04 ± 0.11
Minnedosa	61.0 ± 13.9	283.9 ± 27.3	94.1 ± 21.0	285.2 ± 28.5	155.1 ± 34.1	569.1 ± 51.7	1.78 ± 0.23	1.01 ± 0.08
Fredericton	132.0 ± 53.7	271.5 ± 50.1	60.6 ± 21.3	189.1 ± 19.9	192.6 ± 74.6	460.6 ± 69.1	0.54 ± 0.10	0.72 ± 0.07
Garden average	41.6 ± 7.7	152.7 ± 22.9	58.5 ± 5.2	149.4 ± 18.8	100.0 ± 11.7	302.1 ± 40.8	2.12 ± 0.17	1.15 ± 0.08
ANOVA *P*-value	<0.001	<0.001	0.059	<0.001	0.005	<0.001	<0.001	<0.001

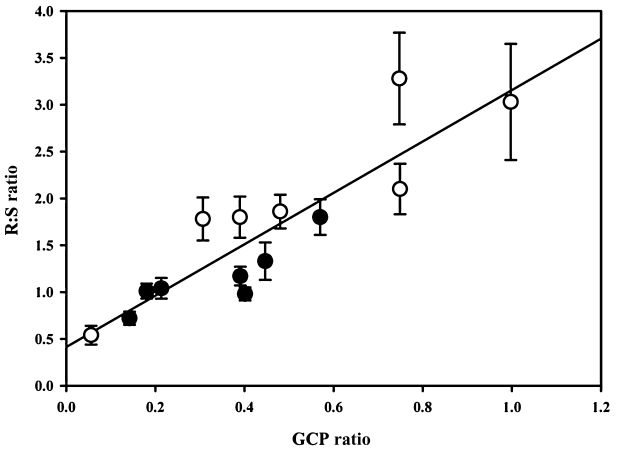

Figure 6. Mean root:shoot (R:S) ratios of populations excavated from both the Vancouver (open circles) and Indian Head (closed circles) common gardens. Data are plotted as a function of green-cover period (GCP) ratio, the number of days in the GCP that occur after bud set divided by the number of days that occur before bud set. Error bars are ± SE.

available in Vancouver (another 1 $^{1}/_{2}$ months) was not only unutilized for tree height growth but the earlier HGC would have partially negated any benefits of an earlier bud flush in spring. This, on average, resulted in an extension of height growth duration of only 2 weeks in Vancouver, a much shorter period than would be expected based on the frost-free period available for growth. Furthermore, for many mid-latitude genotypes, free growth was interrupted in Vancouver by the formation of terminal buds that flushed within a few weeks. There were also many low-latitude trees that had incipient growth cessation but did not come to a full stop to set a lammas bud before normal growth resumed again (not scored).

Spring phenology

In poplar, spring bud flush is not controlled by photoperiod and only occurs upon accumulation of a sufficient heat sum after bud dormancy has been broken by winter chilling (Wareing 1956). Chilling requirements were readily met by near-freezing but not deeply cold winters at the Vancouver site. Spring arrives relatively early; heat sums are accumulated and bud flush is advanced. At both sites, however, genotypes from higher latitudes flush before genotypes from lower latitudes. Northern genotypes may have lower chilling or heat sum requirements, or, because of an earlier bud set in the preceding year, they fulfil these requirements in advance of southern genotypes. Clinal patterns of bud flush with latitude of origin have been observed in many (e.g. Kriebel & Wang 1962; Worrall 1983; Wuehlisch, Krusche & Muhs 1995), but not all (e.g. *Picea sitchensis*; Mimura & Aitken 2007) tree species. Estimates of quantitative trait variance (Q_{ST}) for bud flush are often low (Savolainen, Pyhajarvi & Knurr 2007), as they are in balsam poplar (Keller *et al*. 2011).

Competence to respond

Casual observation suggests that newly flushed shoots of indeterminate trees, such as *Populus*, are not sensitive to photoperiod until they are at least a few weeks old. If this were not the case, then shoots forced to break bud early in a warm environment would begin to form bud scales immediately upon flushing, producing leaves only from predetermined primordia contained within the overwintering bud. Such behaviour would be maladaptive in an early spring. To examine this further, we conducted a controlled environment transfer experiment to determine how long it takes for new spring growth to acquire competency. On average, HGC under an inductive photoperiod (16 h controls) did not occur earlier than 39 d after flushing. Plants moved from 20 to 16 h prior to this age (developmental stage) did not respond to photoperiod immediately either, but afterwards they did. On average, it took 4 d for responsive plants to cease height growth after transfer to an inductive photoperiod. Therefore, we conclude that under our growth chamber conditions, competence to respond to photoperiod was attained after ~35 d of growth. There may be genotypic

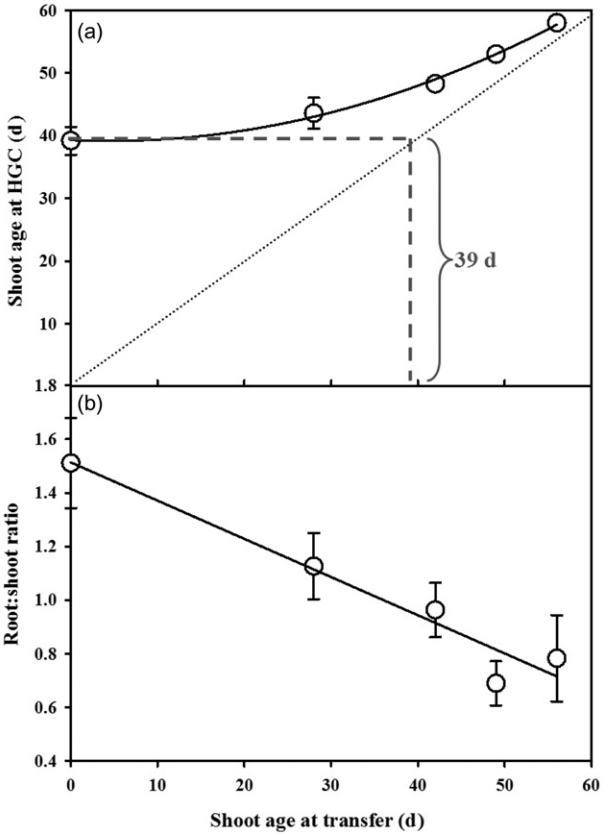

Figure 7. Shoot age (± SE) at which height growth cessation occurs in response to a transfer to short photoperiod (16 h). (a) The dashed lines indicate the minimum number of days (39) after bud flush for the new shoot to cease height growth across a subset of representative provenances. (b) Root:shoot (R:S) ratio (± SE) of the same plants at termination of the experiment (80 d after bud flush).

variation in the length of the non-competent period, but we propose that it is relatively consistent between populations, accounting for the lack of any significant relationship between date of bud set and latitude of origin when HGC occurs before 21 June.

Height growth cessation and second flushing

Mean date of final bud set varied latitudinally among balsam poplar populations, there being a difference of about 13 weeks between the high-latitude and low-latitude populations. Just as for bud flush, clinal variation in bud set has been reported in many tree species (Nienstaedt & Olson 1961; Heide 1974; Morgenstern 1978; Ingvarsson *et al*. 2006; Holliday, Ritland & Aitken 2010; Rohde *et al*. 2011). Several studies on various *Populus* species have clearly shown that the timing of shoot growth cessation accounts for most major differences in height (reviewed by Farmer 1996), and between 85 and 90% of the genetic variance in height growth of *P. balsamifera* (Farmer 1993). Unlike most of these studies, however, the AgCanBaP collection includes a large number of very high-latitude provenances with long summer days. In Vancouver, these populations, as well as many mid-latitude genotypes, were induced, each year, to begin HGC several weeks before the summer solstice. They were therefore responding to photoperiod (which, at the latitude of the common gardens, is always below the critical photoperiod) as they became competent to perceive it. Similarly, Brissette & Barnes (1984) found that *Populus tremuloides* sourced from Alaska stopped shoot growth in mid-June when planted in Michigan. Even in our Indian Head garden, HGC in the northern populations (>56°N) occurred well before normal, as they became competent. The direction of photoperiodic change (increasing versus decreasing day length) is clearly not involved. This is unsurprising given that, in their native environments, spring arrives only a few weeks before the summer solstice. For the most northerly populations, by the time it is warm enough to flush, the days are already close or equal to 24 h. As a consequence, the growing shoots would normally experience only decreasing photoperiods and there would be no selective pressure towards distinguishing the direction of change.

Premature bud set at or near the solstice was not restricted to the northern populations and was observed in many other genotypes. In some case, these buds entered dormancy and did not lammas, whereas the majority went through a second flush. Although, as noted above, the average date of HGC was earlier in Vancouver than at Indian Head, there was a much greater range of response within each population in Vancouver. The average standard deviation about each provenance mean in Vancouver was approximately twice that of Indian Head (± 15.5 versus ±8.5 d, respectively). Most genotypes that either lammased or continued to grow through the solstice, set bud around the same time in both gardens, responding in common to short days later in the growing season. An increase in frequency of bud formation in late July in some genotypes at Vancouver remains unexplained.

Leaf senescence

In comparison to HGC, leaf drop occurred over a much shorter period of time. There were, nonetheless, strong differences between sites and across populations, which interacted with each other. Although leaf senescence cannot precede HGC, the photoperiodic cueing of bud set and leaf senescence are separate events, as demonstrated in European aspen (Luquez *et al*. 2007; Fracheboud *et al*. 2009). Natural photoperiodic regimes demand that there be a greater difference in critical photoperiods for these two events at higher latitudes. Leaves clearly abscise nearer to the autumnal equinox than to the summer solstice in all populations. Because day length is the same at all latitudes at the equinox (12 h), critical photoperiods for leaf senescence are not as strongly differentiated. For northern genotypes in both common gardens, midsummer photoperiods are too short to maintain height growth but are long enough to prevent leaf senescence until a date not much different than it would be in their native habitats. As a consequence, individual leaves live much longer than normal, and the GCPs are greatly extended.

On average, leaf senescence was a little earlier at the Vancouver location than at Indian Head. As with HGC, two conditions must be met to trigger senescence: leaves must be competent and day length must be below the critical threshold. Competence to respond to photoperiod for purposes of leaf senescence presumably develops a few days after HGC (Fracheboud *et al*. 2009), but little information is available on this point. Weather can also influence the date and speed of bud set and leaf senescence in many species (Junttila 1980; Dunlap & Stettler 1996; Kalcsits, Silim & Tanino 2009) and Taylor *et al*. (2008) have reported delayed leaf senescence among low-latitude *Populus* spp. under elevated CO_2. However, the timing of leaf senescence in aspen poplar in both Canada (Barr *et al*. 2004) and Scandinavia (Pudas *et al*. 2008; Fracheboud *et al*. 2009) is insensitive to annual temperature fluctuations, and is triggered on the same day, year after year. There is also a clear effect of leaf age in *Populus*, whereby the oldest leaves yellow first while the youngest neoformed leaves towards the shoot tips yellow last. This may explain why 50% yellowing occurred earlier in Vancouver for southern genotypes because average dates of bud set (and therefore the last dates of new leaf production) occurred earlier than in Indian Head. On the other hand, for the northern genotypes, all leaves are overmature by summer's end and it is clear that only day length delays leaf senescence.

Effects of early bud set on biomass accretion and partitioning to root growth

As expected, we found very large clinal variation in shoot, root and total plant growth, much of which can be ascribed

to variation in bud phenology. Using the same AgCanBap collection, we have previously shown that population differences are much less pronounced when grown under extended days in a greenhouse, and are in fact reversed, with high-latitude populations tending to outperform those from low latitude (Soolanayakanahally *et al*. 2009). Poor growth in Vancouver might suggest other factors (water or nutrients) were limiting, but this common garden area includes native black cottonwood and various hybrid poplars of approximately the same age, and these grow very well on this site. Another maritime balsam poplar population that we did not excavate (Roseville) also grows well in Vancouver. Heights for this population were similar in both common gardens at the end of four years (~3.1 m, $P = 0.503$). Consequently, we propose that most of the growth difference between the two common garden sites is caused by phenological 'stress'. As noted by Farmer (1996), 'major movement south produces a conservative, stunted, non-competitive phenotype'. The additional movement from a continental climate to the maritime coast increases this effect.

Even though there is an overall earlier start to leaf senescence in Vancouver than in Indian Head, the total GCP is longer because of the earlier spring, suggesting an extended season for photosynthetic activity. However, because of the early height growth cessation at Vancouver, any further carbon fixed can clearly not be used towards shoot extension growth but may contribute to secondary growth or, as supported by our growth chamber experiment (Fig. 7b), be exported to the roots (Isebrands *et al*. 1983). This should also be the case where height growth is interrupted by lammas bud formation. Reflecting trends in GCP Ratio (Supporting Information Fig. S1), R:S ratios increased with latitude of origin in both gardens and were particularly extreme in Vancouver (Table 2 and Fig. 6). A notable exception was Fredericton, an eastern maritime provenance. This was the only excavated population originating from a latitude south of Vancouver – it was also the only one to have a lower GCP ratio and, in striking concordance, a lower R:S ratio at this site than at Indian Head. Similar to our observations for balsam poplar, Cannell & Willett (1976) found that R:S ratios of black cottonwood (*P. trichocarpa*) increased with latitude of origin when planted into a common garden. They likewise ascribed this imbalance to premature cessation of height growth.

Our results do not suggest that climate warming will affect carbon partitioning in trees growing in their native habitats unless height growth ceases or is interrupted prior to the solstice, but there are implications for human-assisted migration as an adaptation scenario. It is possible that a phenological mismatch may be avoided by moving photoperiodically appropriate genotypes along climate clines that have an east-west or elevational orientation. On the surface of it, longer growing seasons should boost net carbon fixation and overall tree growth and possibly net ecosystem productivity, particularly in spring. The shorter days that occur late in the growing season contribute less photosynthetic activity, and a longer and warmer autumn may promote carbon loss through respiration (Piao *et al*. 2008). Rigid photoperiodic control of leaf senescence, however, must absolutely limit the potential positive effects of moderate climate warming to the spring. Given more extreme warming, our results suggest that long critical photoperiods and inherent controls on photoperiodic competency may, in combination, prevent the full realization of even these benefits. To illustrate, Fig. 8 presents the expected effects of an early season on balsam poplar phenology at Fort McMurray, Alberta, near the geographic centre of the species range. Because the critical photoperiod is not much shorter than the longest day of the year, spring needs to advance only a few weeks for dormancy induction to begin on the 'wrong side' of the summer solstice. Within-population genetic variation in response to photoperiodic

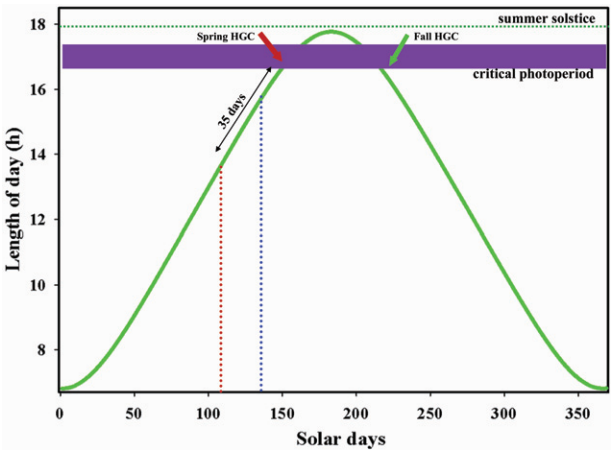

Figure 8. Expected effects of an early spring on bud phenology at Fort McMurray, Canada (56.92°N). The length of day (h) at this latitude is plotted (solid green line) as a function of time of year (solar days). The dotted green line is the maximum day length on 21 June (solar day 183). The purple band represents the critical photoperiod (~1700 h) for the induction of height growth cessation (HGC, denoted by green arrow) in typical Fort McMurray genotypes of native balsam poplar. Spring flush coincides with the accumulation of ~80 degree-days (>5 °C) which, based on 1970–2000 Climate Normals, is achieved about 6 May (solar day 136; dashed blue line). Currently, leaf flush varies by up to 2 weeks on either side of this date, depending on the year. If competency is achieved after 35 d growth, then shoots will be responsive to photoperiod beginning 10 June (solar day 171, again ± 2 weeks). Height growth continues until the critical photoperiod is encountered near 2 August (solar day 232), and ceases ~4 d later (green arrow). With climate warming, if mean dates of spring flush advance by 3 weeks (red dashed line), then shoots become responsive to photoperiod beginning 13 May (solar day 145). This date is still safe because the photoperiod by this time is longer than critical. In a warm year, however, many trees may end up on the wrong side of this threshold and suffer premature height growth cessation and spring bud set (red arrow). They may resume growth through a lammas flush. If mean dates of spring flush are advanced by 5 weeks (not shown), then most trees will be caught in most years, with many individuals entering dormancy and failing to even lammas.

cueing is, however, substantial in balsam poplar and has the potential to buffer climate change impacts on native stands (Olson *et al*., submitted).

CONCLUSIONS

We can account for most of the differences in bud phenology between the two common garden sites based on differences in spring start date, which in turn result in different dates of competency interacting with a fixed photoperiodic regime. Height growth cessation and, to a lesser extent, leaf senescence can be plastic but in a maladaptive direction, occurring earlier and not later. Early bud flush in a warming climate may pose a risk to balsam poplar and perhaps other boreal trees by severely curtailing height growth if competency is achieved before the solstice. Lammas growth can provide a margin of safety in the event of an early spring because the renewed shoot growth is presumably not competent to immediately respond to photoperiod. Even in the absence of a premature bud set, tight photoperiodic control of HGC and leaf senescence will prevent balsam poplar and probably other hardwoods from exploiting an extended autumn. Consequent effects of GCP ratio on carbon partitioning might add to relative respiratory costs, influence drought response or have downstream effects on C cycling and other ecosystem level processes.

ACKNOWLEDGMENTS

The efforts of William (Bill) Schroeder in establishing the original balsam poplar germplasm collection with assistance from others at Agriculture and Agri-Food Canada (AAFC) are wholly appreciated. We thank Don Reynard and Limin Liao for maintenance and phenology scoring of the common gardens. This work was funded by Agroforestry Development Centre, AAFC under the Student Research Affiliated Program (to R.Y.S.) and by the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants Program (to R.D.G.). M.S. received a visiting scientist fellowship (to R.D.G. lab) from Peoples Republic of China.

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Received 3 December 2011; accepted for publication 7 June 2012

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Dates of bud set for all genotypes that did not lammas in 2008, plotted according to provenance (latitude of origin) and common garden location (Vancouver, open circles; Indian Head, closed circles).

Figure S2. Green-cover period ratio (number of post-bud set days over pre-bud set days) in *Populus balsamifera* provenances at Vancouver (open circles) and Indian Head (closed circles). Exponential curve fit is plotted using latitude of origin as the independent variable. Error bars omitted for clarity.

Table S1. Latitude of origin of *Populus balsamifera* provenances used for this study. Provenances marked by† were excavated from both common gardens to determine root:shoot ratio. Provenances marked by * were used in the growth chamber study.