



Aspen Phenology Monitoring in the Central Alaska Network of the National Park Service

Progress Report 2010

Natural Resource Technical Report NPS/CAKN/NRTR—2010/501



ON THE COVER

Top Left (clockwise): Male aspen flower before opening, male aspen flower after opening, fully unfurled and expanded aspen leaves, ripening female aspen flower

Photograph by: Fleur Nicklen and Josh Scott

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Abstract

We examined the phenology, or the timing of biological events, in aspen trees in interior Alaska. Specifically, we observed the dates of leaf out, flowering and fall senescence in aspen in plots in parks within the Central Alaska Network. We first examined six years of aspen phenology observations taken from two very different areas (one a steep, dry, south-facing area and one a flat, mesic area) within Denali National Park. We then compared the phenology of aspen from similar habitats (both flat and mesic) in different parks: Denali National Park and Wrangell St. Elias National Park. We made correlations between climate variables and phenology benchmarks. We also investigated differences in flowering and bud burst between female and male trees.

Generally, we found the two Denali aspen trees had similar phenology in both the spring and fall. The Denali and Wrangell St. Elias aspen trees had different timing for leaf out, but similar timing for senescence. In general we found spring leaf out was highly correlated with late spring temperatures, while the onset of senescence was correlated with a minimum temperature being reached and progression of senescence was correlated with growing season rainfall. Our data do not rule out the importance of photoperiod as a controlling factor in leaf senescence. We also found that male and female trees differ in their timing of flowering and leaf out.

Documenting the timing of biological events in the far north is an important step in simply understanding how trees resolve the conflict between losing leaves to frost and gaining as much photosynthetic energy as possible. Understanding how plants respond to current climatic conditions is critical to predicting how plants may respond as our climate changes.

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1 Introduction

The timing of biological events in the far north is often strictly controlled by physical factors associated with the climate because of the extreme variation in climate norms during the course of the year. Due to the importance of physical factors in regulating physiological processes of northern biota, any future changes in the climate will have far-reaching and profound biological effects. In fact, phenology, or the timing of recurring biological events, has been shown to have important influences on plant fitness (Primack 1980) and as a result may influence species geographic ranges, particularly at their northern limits (Chuine and Beaubien 2001). Phenology has thus been recognized as an important facet of research on global climate change (Menzel and Fabian 1999, Schwartz 1998). We have identified plant phenology as a vital component of our long term vegetation monitoring program (MacCluskie et al. 2005).

The growing season is relatively short in central Alaska, and begins once the sun rises high enough in the sky to warm the air sufficiently to melt the snowpack, and soils thaw to allow plants to take up water and nutrients. The growing season comes to an end when the day-lengths and temperatures dwindle in the latter part of August and freezing temperatures once again become a daily occurrence. In general, the growing season in the lowlands of central Alaska occurs each year between early to mid May and late August or early September. This represents a generalization, and the duration of the growing season varies for different species and in different areas of the landscape. For example, alpine areas often melt out later and thus the onset of spring is delayed in these areas, or wetland sites may experience plant growth later in the year because of the capacity of water to store heat and the reduced influence of late summer draught in these areas. Areas with the earliest inception of growing season occur on steep south-facing slopes in the lowlands where flowering herbs may be encountered as early as mid-April in some years. It should be recognized that the factors that regulate dormancy in plant species are complex and variable, but in the subarctic temperature and day-length are of paramount importance (Samish 1954, Nienstadt 1966).

We began a monitoring program to track one facet of vegetation phenology, the timing of flowering, bud burst, green-up, and foliar senescence of aspen (*Populus tremuloides*) in Denali National Park in 2005. The program was expanded in 2008 to include sites at Eagle on the Yukon River in eastern interior Alaska and at Copper Center in the Copper River basin in south-central Alaska (Figure 1 shows the location of these monitoring stations). In 2010, we added a site adjacent to the Georgeson Botanical Garden on the University of Alaska, Fairbanks Campus. The goal of this program is to detect changes in the timing of key events in the life cycle of this species over time in relation to climate. Because it is likely that the phenology of this species is correlated with many others, at least in a relative sense, this program will provide data on an important ecosystem attribute in the far north that is greater in scope than just species of interest. We chose aspen because it is a very widely distributed species that was monitored in other national and international phenology networks and thus our results can be examined within regional, continental and global contexts (see the following <http://www.eman-rese.ca>; <http://www.plantwatch.ca> ; http://www.usanpn.org/?q=Populus_tremuloides).

2 Methods

2.1 Study Areas

This study has been replicated in four different ecoregions where network staff can readily make observations of aspen trees three times per week – this includes the headquarters areas for each of the three parks in the central Alaska Network – Denali Park, Copper Center, Eagle and most recently Fairbanks (Figure 1). In each of the four locations we chose aspen stands in close proximity to park headquarters because of the need to visit these sites on a regular basis to make phenology observations. Thus, remote locations were not an option for logistical reasons. However, all of the monitoring sites are located in relatively undisturbed natural forest without direct influences from human activities, ensuring these data reflect natural phenological conditions of the study areas.

This program began in April 2005 with the establishment of two aspen phenology monitoring plots in Denali National Park and was expanded to include sites in Eagle and Copper Center in May 2008 (Figure 1 and Table 1). We added the Fairbanks plot in the spring of 2010.

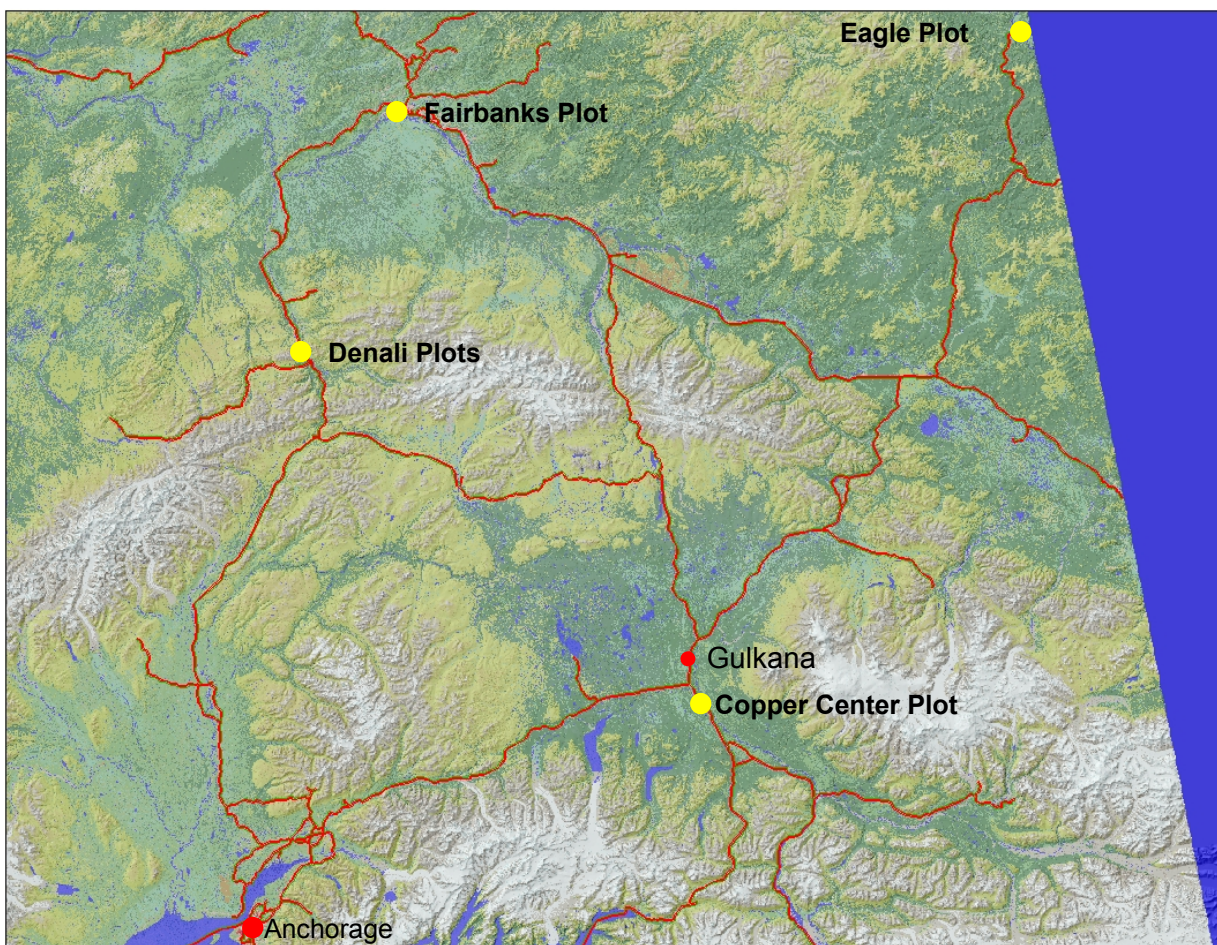


Figure 1. Map of south-central and interior Alaska showing the Central Alaska Network aspen phenology observations sites (yellow dots).

Table 1. The length of phenology records for four stations in the Central Alaska Network aspen phenology monitoring program.

Site Name	2005	2006	2007	2008	2009	2010
Denali Plot 1	Yes	Yes	Yes	Yes	Yes	Yes
Denali Plot 2	Yes	Yes	Yes	Yes	Yes	Yes
Eagle	No	No	No	Yes	No	No
Copper Center	No	No	No	Yes	Yes	Yes
Fairbanks	No	No	No	No	No	Yes

2.1.1 Denali

Two monitoring sites were chosen at random using the park GIS from within aspen-dominated forest communities near the east end of the Park Road that were readily accessible from the road. Plot 1 was installed in a pure stand of relatively small-diameter aspen trees on a moderately steep south-facing slope at 559 m elevation above the park Road at the base of “Government Hill” (Plate 1). Plot 2 was located higher up the slope on a bench supporting more mature, larger-diameter mixed white spruce –aspen forest in a more mesic topographic position at 570 m elevation (Plate 2).



Plate 1. Photograph showing aspen phenology Plot 1 in Denali National Park in early spring. This site supports mixed small-diameter white spruce aspen forest on a dry, moderately steep south-facing slope.



Plate 2. Photograph showing Aspen site 2 in Denali National Park in the early spring. This site supports a mixed white spruce aspen forest on mesic bench area of a south-facing slope.

2.1.2 Copper Center

The Park headquarters and Visitor Center area in Copper Center occupies a young, mature mixed white spruce-aspen stand on a terrace above the Copper river formed by lacustrine sediment from the proglacial Lake Ahtna. The aspen phenology plot in Copper Center is at approximately 410 m elevation, and is located 100m south of the main headquarters building in relatively undisturbed open mixed forest. A photo of the plot vicinity in Copper Center is shown in Plate 3.



Plate 3. Photograph of aspen phenology monitoring site in Copper Center, Alaska near the N.P.S. headquarters in early spring prior to leaf-out. Site supports a mixed white spruce-aspen forest on moderately well-drained lacustrine sediments.

2.1.3 Eagle

The aspen phenology monitoring plot was installed west of the runway and south of the Park headquarters building on a stream terrace above Mission Creek near the town of Eagle at an elevation of about 280 m (Plate 4). The vegetation of this area is similar to that of the other plots in the study with mature aspen trees growing in a mixed forest with white spruce (*Picea glauca*) and a few birches (*Betula neoalaskana*).



Plate 4. Photograph of the aspen phenology monitoring site in Eagle. This site supports mixed aspen-white spruce forest on well-drained alluvial sediments with scattered *Betula neoalaskana*.

2.1.4 Fairbanks

We chose an aspen site located on the grounds of the University of Alaska Fairbanks Georgeson Botanical Garden that is relatively close to NPS headquarters and supports a mixed stand of aspen and spruce very similar to the sites in Denali and Copper Center. This site is located on a gently sloping, south-facing hill (Plate 5).



Plate 5. Photograph of the aspen phenology monitoring site in Fairbanks. This site supports mixed aspen-white spruce forest on well-drained loess deposit.

Table 2. Physical attributes of the five phenology monitoring sites.

	Denali Plot 1	Denali Plot 2	Copper Center	Fairbanks	Eagle
Elevation (m)	559	570	410	178	280
Slope angle (deg)	26°	flat	flat	9°	flat
Aspect (deg)	155°	No aspect	No aspect	185°	No aspect

2.2 Data Collection

Our methods are simple, and while they require some training, reference materials, and equipment, they do not require specialized expertise. At each plot, we selected 12 aspen trees at random from forested locations near park headquarters. Trees were selected by measuring a random distance along a random azimuth from a central location and choosing the nearest live aspen tree of ten cm diameter or greater. We rejected trees that were closer than five meters from another tree already selected for the sample to reduce the likelihood of repeated sampling of genetic individuals (because aspen can form extensive clones). The sample trees were then marked with a numbered tag and a GPS location was recorded for each one.

Observations of each tree were made three times per week during two intervals of the growing season: 1) early spring, beginning prior to the inception of flowering and continuing until leaves are full-sized; and 2) in the fall, beginning prior to the inception of leaf senescence and continuing until 100% of leaves have turned color. We performed the field observations for this study at a standard time each day in all of the sites – as close to 2:00 PM as possible.

Observations of phenological status were recorded for each tree to determine whether specific phenological thresholds were in evidence. Each observation for each phenology state for each tree was made in the form of an answer to a yes/no question. Table 3 shows the phenology benchmarks used for this study. In addition to the phenology observations, two soil temperature readings per tree are made at 10 cm depth (1.5 m from base of tree) and general weather and vegetation observations were recorded for every sampling event. Also, the diameter at breast height (1.37 m) of each tree was recorded each year.

2.3 Climate data

We obtained climate data for the areas including the study plots from established, long term climate stations:

- 1) Denali National Park kennels climate station – located in the park headquarters of Denali National park and Preserve, at 524 m elevation. This climate station is roughly 2km W of and 4 m lower in elevation than the study plots.
- 2) Gulkana weather station – located 20km N of the Copper Center Plot at the Gulkana Airport off the Richardson Hwy. The weather station is approximately 70m higher in elevation (483m) than the Copper Center Plot (410m).
- 3) Fairbanks weather -- comes from the Alaska Climate Research Center (<http://climate.gi.alaska.edu/>). The weather station is located roughly 0.5km NE of the Fairbanks phenology site, on top of the Geophysical institute building on the University of Alaska Fairbanks campus at a similar elevation of 225m.

We calculated period summary statistics and thawing degree days, which is defined as the sum of mean daily temperatures above zero Celsius, using the raw daily weather data from these stations.

2.4 Data Summary and Analysis

The data summary and analysis procedures used to examine patterns in the timing of various phenological events within and among our study sites for this progress report are simple and straightforward. We calculated the percent of trees that reached defined phenological stages (Table 3,4) for sites during each year. This allows us to compare broad trends in “average” phenology of the sampled trees among sites or among years for an individual site. For example, we can compare the numerical date at which 100% of the trees at two different sites have experienced bud burst, or the date by which all of the trees at a given site had had 50% of their leaves turn yellow in the fall. These values can also be compared to temperature and other climate variables to help interpret some of the potential reasons for variation in phenology among years or among sites. We also examined averages of individual tree metrics from different sites, years, and genders to examine variation in time between flowering and leaf out. It should be noted that these data sets are of too short a duration for formal statistical analyses of the observed patterns to be warranted at this time. It should also be noted that we cannot be completely sure that for any specific site we have not sampled a genetic individual more than once, due to the biology of this species, which sends out long below-ground runners and reproduces asexually by clones with abandon. However, we believe the study design is sufficiently robust to allow us to and evaluate inter annual variation in plant phenology and to detect important long term trends in this key ecosystem component.

Table 3. Phenological states recognized for central Alaska Network aspen phenology monitoring program. For each state, the given stage must be in evidence and visible on three separate branches of the main trunk of the tree. The data are binomial and mutually exclusive – the answer is yes or no for each state for each tree in the sample at each sampling date.

Phenological State	Definition
Spring events	
<i>Flowering</i>	
Tree dormant	No evidence of flowering apparent
Catkins Emerging	Are catkins in “pussy willow” stage visible on three different main branches of the tree?
Catkins Open	Are catkins open – for male tree are anthers open and shedding pollen or for female tree are stigmas exerted and receptive?
Catkins Ripe	Are male catkins empty or are female catkins with inflated capsules indicating seeds ripe?
Catkins Falling	Are ripe catkins falling from the tree?
[Sex of Tree]	Are catkins male or female?
<i>Foliage</i>	
Tree Dormant	No evidence of leaf-out occurring.
Leaf Buds Bursting	Leaf buds bursting on at least three main branches of the tree.
Leaves Unfurled	Leaves unfurled on the main branches – full outline of leaves visible with petioles.
Leaves Full-sized	Leaves have reached full size on three main branches of tree.

Fall events

Leaves Green	Less than 25% of leaves on tree showing yellow color.
> 25% of Leaves Yellow	Greater than 25% of leaves on tree have turned yellow.
>50% of Leaves Yellow	Greater than 50% of leaves on have turned yellow.
>75% of eaves Yellow:	Greater than 75% of leaves on tree have turned yellow.
100% of Leaves Yellow	100 % of leaves on tree are turned yellow

From the list of phenological states we detailed in our observations (Table 3), we selected several important benchmarks with which we have conducted our analyses. Because these benchmarks could have a variety of acceptable definitions, we precisely defined our measure of these benchmarks in Table 4. We defined ‘bud burst’ as the date by which half or more of the trees in the plot had buds bursting on the main branches. We called the ‘growing season start’ the date by which at least half of the trees in the plot had unfurled leaves and ‘complete green-up’ the date by which all of the trees in the plot had unfurled leaves. Our benchmarks for reproductive phenology include ‘first flowering’, ‘full flower’ and ‘fruiting’ and are defined respectively as the date by which at least one tree in the plot had open catkins, the date by which all of the flowering trees in the plot had open catkins, and the date by which female catkins are green and ripe and male catkins were empty and falling from the tree. For the fall benchmarks, we called the date by which one tree in the plot had 25% yellow leaves as ‘first yellow’. We defined the ‘growing season end’ as the date by which all of the trees in the plot had at least 50% yellow leaves and ‘complete senescence’ as when all of the trees in the plot were completely yellow.

Table 4. Definition of phenology benchmarks used in this report:

Phenology Benchmark	Definition
Bud Burst	Date on which 50% of trees in plot had leaf buds bursting.
Growing Season Start	Date on which at least 50% of the trees had unfurled leaves
Complete Green-up	Date on which all trees in plot had unfurled leaves
First Flowering	Date by which at least one tree in the plot had open catkins
Full Flowering	Date on which all of the trees in the plot had open catkins
Fruiting	Date by which ripe female catkins and empty or falling male catkins were observed on all (flowering) trees in plot
First Yellow	Date on which at least one tree in the plot had 25% yellow leaves
Growing Season End	Date by which 100% of the trees in the plot had 50% yellow leaves
Complete Senescence	Date by which 100% of the trees in the plot had 100% yellow leaves

3 Results

Phenology observations were recorded at two plots in Denali NP for six consecutive years (starting in 2005) and for three consecutive years in Copper Center near the headquarters of Wrangell-St. Elias NP (starting in 2008). We began observations in Fairbanks in 2010 and have one season's data for this location. Aspen phenology observations were recorded at a plot in Eagle on the Yukon River in eastern interior Alaska in 2008 only. We first present results for the six-year record of observations in the two Denali sites and then compare results from Denali and Copper Center during the three years of concurrent observations. We then examine data from individual trees to explore variation in flowering between individuals, sexes and plot location.

3.1 Tree diameters of study trees in four plots

The average tree diameters at breast height (dbh) in the five plots were very similar across study areas, with a grand mean of the plot means of 16.4 cm dbh. The only plot that deviated from the grand mean dbh by more than 4 cm was Denali plot #1, which was located on steep south-facing hillside and the 10 cm dbh tree inclusion criterion was relaxed for this location because of the small tree sizes in this xeric, moderately steep, south-facing slope. The mean dbh of the trees in Denali Plot 1 was 11.2 cm (standard error ± 1.22 cm) whereas the mean dbh of the trees in Denali Plot 2 was 16.9 cm (se ± 1.12 cm). The mean dbh of the trees in the Copper Center plot was 18.6 cm (se ± 1.67 cm). The mean dbh for the aspen trees in the Eagle plot was 15.8 (± 1.00 cm). The mean diameter of the sampled trees in the Fairbanks plot was 19.7 (se ± 0.66 cm).

3.2 Aspen phenology and climate in two Denali Plots 2005 – 2010

3.2.1 *Spring green-up and flowering*

During 2005 through 2010 spring green-up from bud burst to complete green-up of the Aspen trees in our two Denali plots occurred between the dates of May 9 and June 2 (Table 5). This represents duration of 25 days. The earliest date for aspen bud burst was May 9, 2005 (day 129), the date at which aspen trees in both Denali plots experienced bud burst (Table 5). Green-up progressed rapidly in 2005 and by May 11, both plots had reached the stage of complete green-up.; this was the earliest date for leaves unfurling out of the six years for both plots. Bud burst and green-up occurred both early and rapidly in 2005 as compared to all of the other years in the study thus far. Bud burst occurred in the fourth week of May for both plots in years 2006, 2007 and 2008 and in the third week of May in the last two years of observations: 2009 and 2010. The latest bud burst we observed occurred in 2006 when bud burst was observed on May 26 (day 146) in Plot 1: two and a half weeks (17 days) later than 2005. The latest leaf unfurling occurred in 2008; leaves did not unfurl on all study trees until June 2 in Plot 1 and May 30 in Plot 2: about three weeks later than in 2005. This suggests the mean green-up date for aspen trees in this area was both later and progressed more slowly, on average, in 2008 as compared to 2005. We have not tested this statistically, but there appear to be major differences between these two years in both the timing and in the rate of progression of bud burst in the Denali plots.

Table 5. Dates for selected early season aspen leaf-out phenology benchmarks for the period 2005-2010 in two plots in Denali National Park, Alaska and for the period 2008-2010 for one plot in Wrangell-St. Elias National Park, Alaska (numeric date shown in parenthesis).

Year	Bud Burst	Start of the Growing Season	Complete Green-up	Number of days to complete green-up
Denali Plot #1				
2005	May 9 (129)	May 11 (131)	May 11 (131)	2 days
2006	May 26 (146)	May 26 (146)	May 26 (146)	0 days
2007	May 21 (141)	May 23 (143)	May 23 (143)	2 days
2008	May 23 (144)	May 30 (151)	June 2 (154)	10 days
2009	May 15 (135)	May 25 (145)	May 25 (145)	10 days
2010	May 19 (139)	May 21 (141)	May 21 (141)	2 days
Denali Plot #2				
2005	May 9 (129)	May 11 (131)	May 11 (131)	2 days
2006	May 24 (144)	May 31 (151)	May 31 (151)	7 days
2007	May 21 (141)	May 23 (143)	May 23 (143)	5 days
2008	May 23 (144)	May 28 (149)	May 30 (151)	7 days
2009	May 18 (138)	May 25 (145)	May 25 (145)	7 days
2010	May 19 (139)	May 19 (139)	May 21 (141)*	2 days
Difference between two Denali Plots				
2005	0 days	0 days	0 days	0 days
2006	2 days	5 days	5 days	7 days
2007	0 days	0 days	0 days	3 days
2008	0 days	2 days	3 days	3 days
2009	3 days	0 days	0 days	3 days
2010	0 days	2 days	0 days	0 days

*Date of 92% of trees with leaves unfurled (100% not recorded); by next observation (May 24(141)) all unfurled and full-sized.

Whereas the dates of aspen green-up stages varied from year to year in this period, the timing of annual bud burst and foliage maturation in the two Denali plots was highly synchronous over the period (Table 5). The date of bud burst was identical in the two plots for all years except 2006 when bud burst was two days earlier in Plot 2 and 2009 when bud burst was three days earlier in Plot 1 (Table 5). Although buds burst two days later in Plot 1 than Plot 2 in 2006, bud burst and unfurling progressed rapidly in Plot 1 and slowly in Plot 2 so that the date at which 100% of the trees had unfurled leaves was actually 5 days earlier in Plot 1 than Plot 2 (Table 5). In 2009, when buds burst three days later in Plot 2 than Plot 1, leaf development progressed faster in Plot 2 so that both plots had 100% unfurled leaves on the same date (Table 5). Thus, although there were minor differences between dates of bud burst and leaf unfurling, it is likely there were no substantial differences in the timing of the trees reaching their full photosynthetic potential in these two study populations. This is noteworthy given the differing ecological circumstances of the two plots, one being located on a steep, dry hillside that loses its snowpack quite early (Plot 1) and the other being located on a mesic and protected bench that receives less solar radiation and tends to maintain its snowpack longer in the a spring (Plot 2).

Averaged over the six year observation period, the mean date for bud burst was the same for both plots: May 19 (day 139 of the year; Table 6). The mean date for the start of the growing season was also identical in the two plots: May 23 (day 143 of the year; Table 6). The number of days it took trees to progress from bud burst to complete green-up ranged from zero days to 10 days

(Table 5), but the mean number of days to green-up was very similar between the two plots with a mean 4.3 days in Plot 1 and 5 days in Plot 2 (Table 6).

Table 6. Descriptive statistics for numerical dates of plot average bud-burst attributes reported in Table 3.

Plot	Mean	Std. Deviation	CV	Range
Bud burst				
Plot #1	139.0	6.23	4.48	17 days
Plot #2	139.17	5.56	4.0	15 days
Start of Growing Season				
Plot #1	142.83	6.71	4.65	20 days
Plot #2	143.0	7.27	5.08	20 days
Complete Green-up				
Plot #1	143.33	7.5	5.23	23 days
Plot #2	143.67	7.45	5.18	20 days
# days for green-up				
Plot #1	4.33	4.46	102.86	10 days
Plot #2	5.0	2.45	48.99	5 days

Aspen trees in this study flowered in three of the six years in the observation period: 2005, 2008 and 2010. Full flowering occurred earlier in 2005 than in either 2008 or 2010 (Table 7). All of the trees had open catkins by May 2, 2005 in Plot 1 and May 4, 2005 in Plot 2; whereas, it was May 12 before all trees were flowering in Plot 1 in 2008 and May 14 before all trees were flowering in Plot 2 in 2008 and both plots in 2010. Only a subset of trees flowered in both plots in 2008 and 2010 (9 trees in Plot 1 and 4 trees in Plot 2 flowered in 2008, 11 trees flowered in Plots 1 and 2 in 2010). As with green-up, the two plots were highly synchronous in the time of full flower, only varying from each other by a maximum of two days. It will be interesting to track the inter-annual patterns in flowering through time and perhaps gain insights as to the growing season conditions that promote flowering in the study population trees. It is most likely that the primary determinants of flowering are related to the physiological status of the trees in the year prior to a flowering event. The inception of flowering is probably a function of resource accumulation during the previous growing season, and thus the conditions of this growing season such as precipitation, temperature, growing season length, and perhaps nutrient status are likely determinative.

Table 7. Dates for selected early season aspen flowering phenology benchmarks for the period 2005-2008 in the two plots in Denali National Park, Alaska (number shown in parenthesis is the corresponding numeric date).

Year	First Flowering	Full Flowering
Plot One		
2005	(before) April 16 (106)	May 2 (122)
2006	No flowering	No flowering
2007	No flowering	No flowering
2008	(before) April 22 (113) ++	May 12 (133) ++
2009	No flowering	No flowering
2010	April 7 (97)	May 14 (134) ++
Plot Two		
2005	May 2 (122)	May 4 (124)
2006	No flowering	No flowering
2007	No flowering	No flowering
2008	(before) April 22 (113)	May 14 (135) ++
2009	No flowering	No flowering
2010	April 7 (97)	May 14 (134) ++
Difference		
2005	>16 days?	2 days
2006	None	None
2007	None	None
2008	0 days?	2 days
2009	None	None
2010	0 days	0 days

++ in 2008, 9 out of 12 trees in Plot 1 flowered and 4 out of 12 trees in Plot #2 flowered; in 2010 11 out of 12 trees flowered in Plots # 1 and #2.

3.2.2 Leaf Senescence

Over the six years of phenology observations in Denali the process of aspen leaf senescence has occurred between the dates of August 14 and September 17 (Table 8). During our six years of observations, the earliest ‘first yellow’ leaves occurred on August 14 (day 227 of the year) in Plot 2 during 2008 and the latest ‘first yellow’ leaves occurred on September 3 (day 246 of the year) in Plot 2 during 2007 (Table 8). This is a difference of 19 days in the timing of fall onset among these two years from Plot 2. The date marking the end of the growing season also ranged by 19 days: the end of the growing season occurred as early as August 29, 2006 (day 241) in Plot 1 and as late as September 17, 2007 (day 260) in Plot 2 (Table 8).

The most rapid progression from the start to completion of foliar senescence for the trees in this study was four days. This occurred in Plot 1 during 2006 with the ‘first yellow’ observed on August 25 and complete senescence occurring by August 29 (Table 8). It did not take much longer to complete leaf senescence in 2006 in Plot 2, in which ‘first yellow’ was reached on August 29, and the trees were completely senesced by September 4. The most prolonged period of senescence, 27 days, occurred in 2008 in Plot 2 during which ‘first yellow’ began on August 14 and complete senescence occurred on September 10.

Table 8. Dates for selected late season aspen leaf senescence benchmarks during the period 2005-2008 in the two plots in Denali National Park, Alaska (number shown in parenthesis is the corresponding numeric date).

Plot	First Yellow	End of the Growing Season	Complete Senescence	Number of days to complete senescence
Plot One				
2005	August 19 (231)	Sept. 2 (245)	Sept. 9 (252)	21 days
2006	August 25 (237)	August 29 (241)	August 29 (241)	4 days
2007	August 31 (243)	Sept. 3 (246)	Sept. 10 (253)	10 days
2008	August 18 (231)	Sept. 5 (249)	Sept. 8 (252)	21 days
2009	August 26 (238)	Sept. 9 (250)	Sept. 14 (257)	19 days
2010	August 30 (242)	Sept. 10 (253)	Sept. 10 (253)	11 days
Plot two				
2005	Sept. 2 (245)	Sept. 2 (245)	Sept. 9 (252)	7 days
2006	August 29 (241)	August 29 (241)	Sept. 4 (247)	6 days
2007	Sept. 3 (246)	Sept. 10 (253)	Sept. 17 (260)	14 days
2008	August 14 (227)	Sept. 10 (254)	Sept. 10 (254)	27 days
2009	August 19 (231)	Sept. 14 (257)	Sept. 14 (257)	26 days
2010	August 23 (235)	Sept. 10 (253)	After Sept 10 (253)	>18days
Difference				
2005	14 days	0 days	0 days	14 days
2006	4 days	0 days	6 days	2 days
2007	3 days	7 days	7 days	4 days
2008	4 days	5 days	2 days	6 days
2009	7 days	7 days	0 days	7 days
2010	7 days	0 days	>0 days?	>7 days

The date of ‘first yellow’ tended to vary among the two plots on any given year, with differences between the plots ranging from 3 to 14 days (Table 8). Averaged over the six years, however, the mean date for ‘first yellow’ was the same for both plots: August 25 (day 237) (Table 9). Senescence tended to progress a little slower in the more mesic, protected Plot 2 than in dry, south-exposed Plot 1. On average, the number of days required for trees in study plots to reach complete senescence from the ‘first yellow’ observation was 14.3 days in Plot 1 and 16.3 days in Plot 2 (Table 9). In general, there was greater range in observations among individuals in the both the timing and duration of leaf senescence in Plot 2 as compared with Plot 1 (Table 9). This is probably related to two factors: the larger size of the trees in Plot 2 and the fact that drought stress is probably an important factor affecting all of the trees in Plot 1 and constraining the timing of senescence more than the well-watered area of Plot 2.

Table 9. Descriptive statistics for numerical dates of plot average bud-burst attributes reported in Table 6.

Plot	Mean	Std. Deviation	CV	Range in observations
First Yellow				
Plot #1	237.0	5.18	2.18	12 days
Plot #2	237.5	7.74	3.26	19 days
End of the Growing Season				
Plot #1	247.33	4.23	1.71	12 days
Plot #2	250.5	6.12	2.44	16 days
Complete Senescence				
Plot #1	251.33	5.39	2.15	12 days
Plot #2	253.83	4.45	1.75	13 days
# days for leaf senescence				
Plot #1	14.33	7.03	49.07	17 days
Plot #2	16.33	9.05	55.4	21 days

3.2.3 Growing season length

We defined the start of the growing season for a plot to be the date at which 50% of trees reached the ‘leaves unfurling’ stage and the end of the growing season as the date at which 100% of the trees had 50% of their leaves changed from green to yellow (Table 6). These benchmarks were chosen because they should bracket the period during which the foliage of the trees in each plot are actively engaged in carbon acquisition through photosynthesis (foliage is specified because aspen bark is also photosynthetic tissue). Examining the combined variations in spring green-up and fall senescence we observed over this period, we find that the longest growing season was approximately 114 days in 2005 for both plots (Figure 2), and the shortest growing season was 90 days in 2006 at Plot 2 (growing season length was 95 days at Plot 1 in 2006). The maximum difference in growing season length for Plot 1 was 19 days (114 days vs. 95 days) and for Plot 2 the maximum difference in growing season length during this period was 24 days (114 vs. 90 days). Mean growing season length for Plot 1 was 104.5 days and mean growing season length was 107.5 days at Plot 2. Thus the difference in growing season lengths observed in this six year data set was between 18% and 22% of the average growing season length for these plots for the period between 2005 and 2010 (that is, 19 days/ 104.5 days and 24 days/107.5 days). This represents a considerable difference in the time available for growth and development of plants among years, and there would potentially be many ecological consequences of such substantial variations among growing seasons.

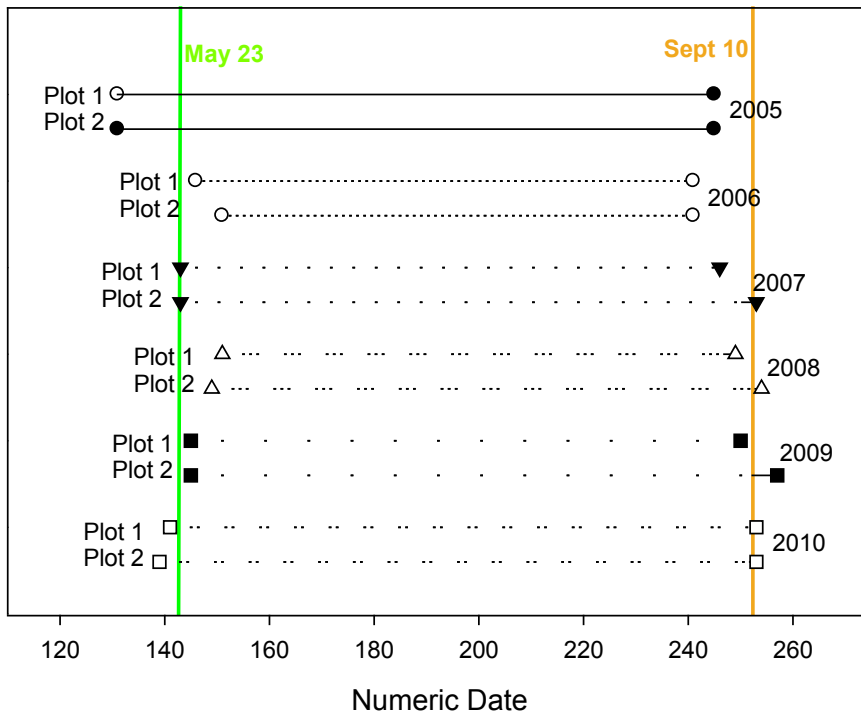


Figure 2. Schematic showing the observed growing season length for aspen trees in Denali Plot 1 and Plot 2 over the period 2005-2010. Vertical lines with date labels show the mean dates for growing season start and end for the plots over the 6-year period.

3.2.4 Variation in early-season climate variables in Denali across sample period 2005 - 2010

The snow-free date at Denali Park headquarters weather station varied between May 2, 2007, the earliest date in the period, and May 12, 2006, the latest snow-free date for the period (Table 10). Mean daily temperature during April was generally below freezing during the years of observation with the exception of 2007 during which the mean temperature in April was 1.32° C, the warmest average temperature for April over the period. The coldest April in this period occurred in 2008 with a mean temperature of -3.85° C. The warmest May average daily temperature over this period was 8.8° C which occurred in 2005 and the coldest average daily temperature for May over this period was 5.03° C observed in 2008 (Table 10). In addition, May 2005 had the greatest accumulation of thawing degree days (273.1) over this period. In general, then, for early season temperatures, the years 2005 and 2010 were warmer than average and 2008 was the coldest on average. Years 2006, 2007 and 2009 had early season temperatures close to the average for the observation period.

Table 10. Summary of selected early-season climate variables from Denali Park headquarters weather station, Alaska for the period 2005 – 2008. Soil Temperatures were taken at the aspen plots while the phenology observations were made.

Year	Snow-free date	Mean Air Temp (°C) during:				Sum of thawing DD for May	Mean May soil temp: Plot 1	Mean May soil temp: Plot 2
		April	May	May 1- Bud Burst	May 1 to Growing Season Start			
2005	May 3	-1.65	8.81	6.81	7.42	273.06	6.22	0.66
2006	May 12	-3.65	6.68	4.95	5.43	208.61	4.27	0.31
2007	May 2	1.32	7.07	5.38	5.68	219.17	5.08	0.74
2008	May 9	-3.85	5.03	4.91	5.10	158.06	2.09	-0.10
2009	May 4	-2.88	6.83	5.63	6.27	211.67	2.38	-0.43
2010	May 4	-1.10	7.52	4.12	4.89	235.28	3.99	0.61
mean	May 5/6	-1.97	6.99	5.30	5.80	217.64	4.01	0.29

The mean May soil temperatures for the two plots were dramatically different over the period, with a mean of 4.01° C in Plot 1 and a mean of 0.29° C in Plot 2 (Table 10 and Figure 3). These soil temperatures were recorded at the time of sampling at a depth of 10cm near each observed tree in the two Denali aspen plots. Mean May soil temperatures in Plot 1 were warmer and relatively variable, ranging 2.09 to 6.22° C as compared to Plot 2, where mean soil temperatures varied only between -0.43 to 0.66° C.. These differences reflect dramatically different solar energy receipts resulting from the differing topographic positions of the two plot locations. Denali Plot 1 is located on a steep, south-facing slope with high radiation receipts and large diurnal fluctuations in temperature, whereas Plot 2 is located on a relatively level bench with considerably more shading and less solar radiation reaching the soil surface.

It is noteworthy, that despite the very different soil microclimates in the two plots, the date of leaf emergence was extremely similar between the two sites (Figure 3) during this study. For example, in 2007 100% of the trees in both plots had unfurling leaves on May 23 (numerical day 143) even though the soil temperature was 9.2° C in plot 1 and only 1.3° C in plot 2 (Figure 3).

These soil data also show differences in years in the progression of soil warming during spring (Figure 3). For both plots, mean soil temperatures in 2008 and 2009 were the coldest recorded for the period for both plots throughout the spring observation period (Figure 3). In 2005, on the other hand, soil temperatures warmed to above freezing by earlier than in any other year during the period (April 27 in Plot 1 and May 2 in Plot 2).

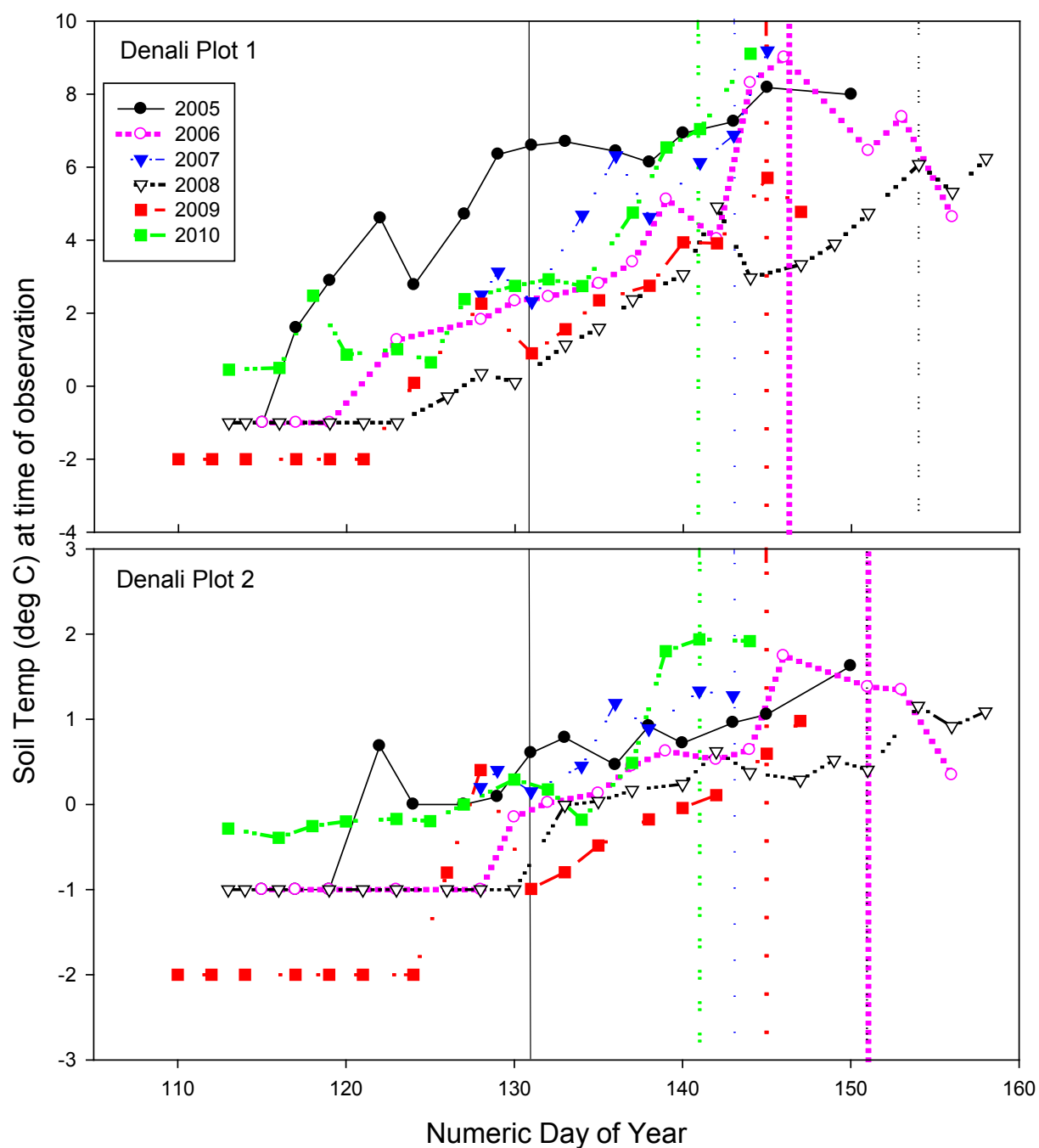


Figure 3. Each point represents the average of soil temperatures taken near each tree during the time of observations. Vertical lines represent the date at which complete green-up was reached for each plot for each year. Vertical line color and pattern match the color and pattern of the soil temperatures for a particular year.

3.2.5 Variation in late-season climate variables in Denali across sample period 2005 – 2010

The average daily temperature for the period beginning August first and including the entire period until the end of the aspen growing season across all six years was 10.8° C (Table 11). The lowest mean temperatures for this period occurred in 2008 (2.7 ° C) and the highest occurred in 2007 (5.93° C). The temperature reached 0.56° C on August 12, 2008, which was the earliest that the temperature hit 2° C or colder in the month of August over this span of time. The latest that this temperature benchmark was reached was August 31 in 2007 (Table 8).

The average daily temperature for discrete period of Aug 15 to Sept 15 across all six years was 9.35°C and the average daily minimum temperature for the same period was 3.16°C (Table 11)

Table 11. Summary of selected late-season climate variables from Denali Park headquarters weather station for the period 2005 – 2008.

Year	Mean temp Aug1-Growing Season End	Mean Min temp Aug1-Growing Season End	Mean temp Aug 15 to Sept 15	Mean Min temp Aug 15 to Sept 15	First date minimum daily temp. < 2° C	Total precip. May 1 to Aug 31
2005	12.40° C	5.59° C	9.20° C	3.47° C	Aug. 19 (231; -1.11° C)	23.47 cm
2006	9.88° C	4.98° C	8.37° C	3.37° C	Aug. 21 (233; 1.67° C)	24.61 cm
2007	12.63° C	5.93° C	11.29° C	3.77° C	Aug. 31 (243; 1.67° C)	21.21 cm
2008	9.16° C	2.70° C	8.95° C	2.06° C	Aug. 9 (222; 1.67° C)	25.70 cm
2009	9.35° C	3.62° C	8.43° C	2.94° C	Aug. 10 (222; 1.11° C)*	17.55 cm
2010	11.17° C	5.03° C	9.85° C	3.97° C	Aug. 21 (233; 1.67° C)	19.53 cm
mean	10.76° C	4.62° C	9.35° C	3.16° C	Aug 18/19 (230.6)	22.01 cm

* A minimum temperature of 0° C was reached on Aug 2, 2009, but this reading was considered too early to impact senescence (Figure 3).

Total precipitation during the growing season varied from a low of 17.6cm in 2009 to a high of 25.7cm in 2008 (Table 11). Mean daily temperatures from August 1 to the end of the growing season for our study trees varied from a low of 9.2° C in 2008 to a high of 12.6° C in 2007 (Table 11).

It is worth noting that for each year in this study, our data suggest that senescence in these study populations is correlated to daily temperature reading dipping below the 2° C mark. In all but one year (2009), we observed at least one aspen tree with more than 25% of its leaves yellowed within four days once the minimum temperature for the day was lower than 2° C (Figure 4). Temperatures fluctuated dramatically in early August of 2009, with an early 0° C low reached on August 2 followed by a week of high temperatures above 10° C (Figure 4). On August 10 the temperature dropped again to a low of 1.11° C. It was a full nine days after this low that the first tree with yellow leaves was seen (Figure 4). Aside from the anomalous 0° C on Aug 2, 2009, the earliest date that 2° C threshold was crossed during this period was Aug. 9, 2008 and the first indication of fall onset in the study trees also occurred first in 2008 (Table 8 and Figure 4). Although ‘first yellow’ initiated earlier in 2008, foliage senescence progressed the fastest in 2006, during which the trees went from having the first yellow leaves to complete senescence in four days in Plot 1 and six days in Plot 2 (Table 8). The average minimum temperatures during early fall 2006 and 2008 were similar (Table 11), but there were four days in 2006 when the

temperatures dropped below freezing versus only one sub-freezing day in 2008 (Figure 4), perhaps accounting for some of this difference in the rapidity of senescence.

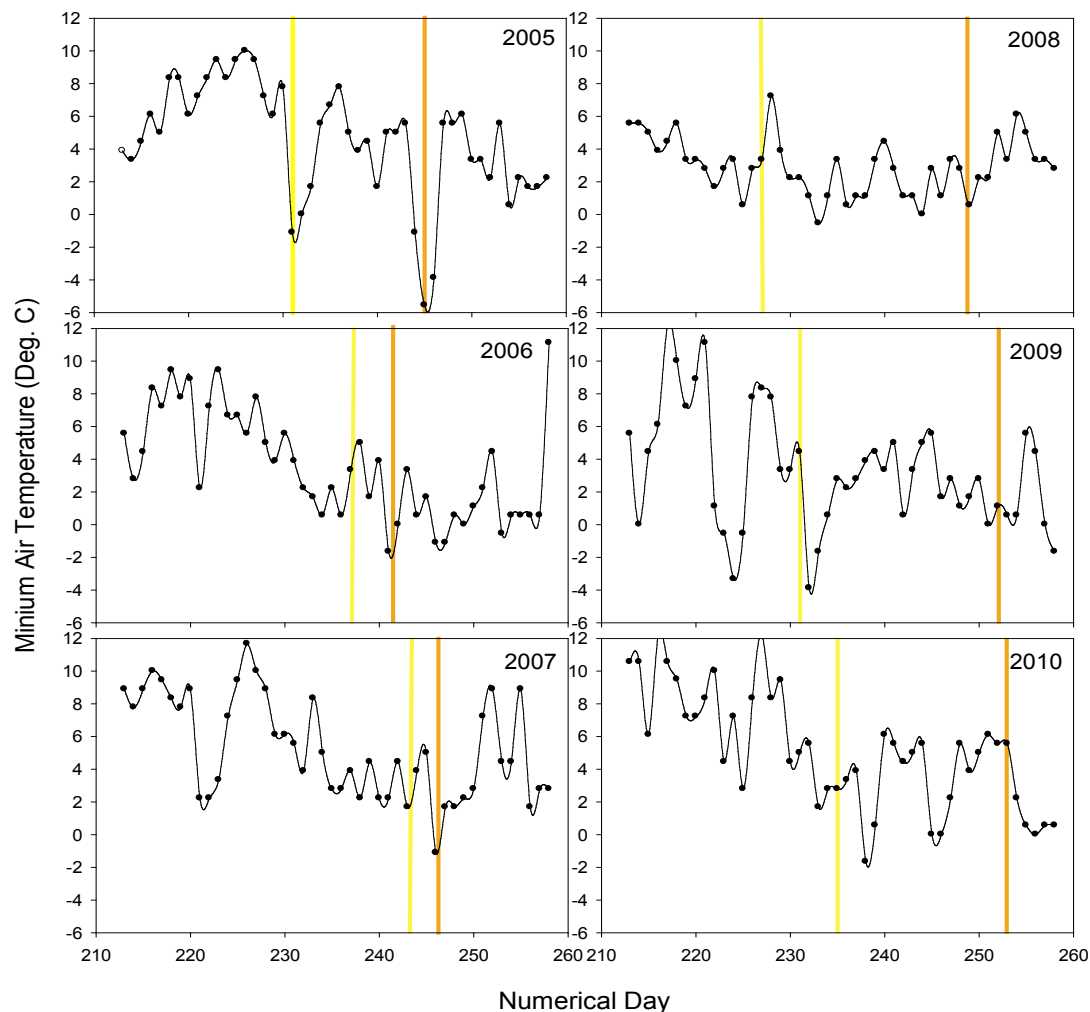


Figure 4. Six air temperature plots showing the minimum daily temperatures recorded for the period Aug 1 – September 15 at the Denali National Park Headquarters weather station for the years 2005 - 2010. The two vertical lines show dates at which the ‘first yellow’ leaves were observed (yellow) and the end of the growing season (orange). If the date at which these phenology benchmarks were reached differed between plots, the earlier date was used. Note that the scales on both exes for all of the plots are identical, allowing gross visual comparisons to be made among the different graphs.

3.3 Aspen Phenology and Climate variables in Denali and Copper Center Plots

3.3.1 Spring green-up and flowering

There are three years of phenology observations from the Copper Center plot. This plot is similar to Denali Plot 2 because it is on flat ground on a bench above a south-facing slope with a similar mix of aspen and white spruce. To investigate how phenology differs between these similar

habitats located in different areas of the state, we compared the observations from the Copper Center Plot and the Denali Plot 2 for the three years for which there are concurrent observations.

In general we found that the process of aspen green-up occurred at an earlier date in the Copper Center plot as compared to Denali Plot 2. On average, bud burst occurred ten days earlier, the growing season started 8 days earlier, and complete green up was five days earlier in the Copper Center Plot compared to the Denali Plot 2 (Table 12). Specifically, buds burst on trees in the Copper Center Plot eight, fourteen and seven days earlier, respectively, than the trees in the Denali Plot 2 for the three years of observations (Table 12). The start of the growing season was earlier in Copper Center than Denali by nine days in 2008 and fourteen days in 2009, but occurred on the same day in 2010 (Table 12). Complete green up also occurred nine days earlier in Copper Center than Denali during 2008, seven days earlier in Copper Center than Denali in 2009 and on the same date during 2010 (Table 12). Leaf unfurling progressed rapidly in Denali in 2010, so although buds burst seven days earlier in Copper Center than in Denali, the growing season and complete green up started on the same day in both plots: May 19 and May 21 respectively (Table 12).

Table 12. Dates for selected early season aspen leaf-out phenology benchmarks in four plots in interior Alaska during 2008 (numeric date shown in parenthesis).

Location	Year	Bud Burst	Growing Season Start	Complete Green-up	# Days to complete green-up
Copper Center	2008	May 15 (136)	May 19 (140)	May 21 (142)	6 days
Copper Center	2009	May 4 (124)	May 11 (131)	May 18 (138)	14 days
Copper Center	2010	May 12 (132)	May 19 (139)	May 21 (141)	9 days
mean		May 10 (131)	May 16 (137)	May 20 (140)	9.6 days
Denali Plot 2	2008	May 23 (144)	May 28 (149)	May 30 (151)	7 days
Denali Plot 2	2009	May 18 (138)	May 25 (145)	May 25 (145)	7 days
Denali Plot 2	2010	May 19 (139)	May 19 (139)	May 21 (141)*	2 days
mean		May 20 (140)	May 24 (144)	May 25 (146)	5.3 days

*Date of 92% of trees with leaves unfurled (100% not recorded); by next observation (May 24(141)) all unfurled and full-sized.

The number of trees that flowered was inconsistent and the date of flowering was highly variable for both the Copper Center Plot and Denali Plot 2 (Table 13). In Copper Center, only one tree flowered in 2008 and 2009 (different tree in both years) and eight of twelve trees flowered in 2010. In Denali Plot 2, four of twelve trees flowered in 2008, no trees flowered in 2009 and all but one tree flowered in 2010. The date of the earliest unopened catkin seen in the Copper Center Plot varied from April 15 in 2010 to a late date of May 12 2008. In none of the years and neither of the two plots did all of the trees flower. The date by which the few flowering trees all had open catkins varied between an early date of April 27, 2009 to a late date of May 19, 2008 in Copper Center, while in the Denali Plot 2 the date of full flowering occurred on May 14 in both years of flowering (Table 13).

Table 13. Dates for selected early season aspen flowering phenology benchmarks in four plots in interior Alaska (number shown in parenthesis is the corresponding numeric date).

Location	Year	First Flowering	Full Flowering
Copper C.	2008	May 12 (133)	Only one tree flowered-open catkins May 19 (140)
Copper C.	2009	April 21 (111)	Only one tree flowered-open catkins Apr 27 (117)
Copper C.	2010	April 15 (105)	8 of 12 trees flowered-open catkins May 3 (123)
Denali Plot 2	2008	(before) April 22 (113)	4 of 12 trees flowered-open catkins May 14 (135)
Denali Plot 2	2009	No flowering	No flowering
Denali Plot 2	2010	April 7 (97)	11 of 12 trees flowered-open catkins May 14 (134)

3.3.2 Leaf senescence

The difference in the timing of leaf senescence between the Copper Center Plot and Denali Plot 2 was less pronounced than the differences we observed in the timing of green-up between the two plots. Averaged across the three years of observations, both ‘first yellow’ and ‘complete senescence’ occurred two and a half days later in the Copper Center Plot than in Denali Plot 2 (Table 14). The end of the growing season, however, averaged two days earlier in Copper Center relative to Denali (Table 14). This suggests that the progression from ‘first yellow’ to all trees at least 50% yellow happens more quickly in the Copper Center Plot than the Denali Plot 2 (by 4.6 days on average), but that the progression from trees 50% yellow to complete senescence happens more quickly in Denali Plot 2 than in Copper Center (by 4.4 days on average; Table 14).

Table 14. Dates for selected late season aspen leaf senescence phenology benchmarks in the two plots in Denali National Park and Preserve, Alaska (number shown in parenthesis is the corresponding numeric date).

Location	Year	First Yellow	Growing Season End	Complete Senescence
Copper C.	2008	Aug. 18 (231)	Sept. 5 (249)	Sept. 10 (254)
Copper C.	2009	Aug. 26 (238)	Sept. 10 (253)	Sept. 14 (257)
Copper C.	2010	Aug. 20 (232)	Sept. 13 (256)	Sept. 17 (260)
mean		Aug 21 (233.6)	Sept. 9 (252.6)	Sept. 14 (257)
Denali Plot 2	2008	August 14 (227)	Sept. 10 (254)	Sept. 10 (254)
Denali Plot 2	2009	August 19 (231)	Sept. 14 (257)	Sept. 14 (257)
Denali Plot 2	2010	August 23 (235)	Sept. 10 (253)	After Sept 10 (253)
mean		Aug. 18/19 (231)	Sept. 11/12 (254.6)	Sept. 11/12 (254.6)

3.3.3 Growing season length

The mean growing season length for the period 2008-2010 was over 5% longer in Copper Center than Denali Plot 2 growing season: 116 days in the Copper Center Plot and 110 days in Denali Plot 2 (Figure 5). The main difference in growing season length between the two plots occurred during spring, where the start of the growing season began seven days earlier in the Copper Center Plot than the Denali Plot 2. Conversely, the two plots had very similar average dates by which all of the trees in the plots had at least 50% yellow leaves, which was September 9 (252.6) in Copper Center and September 11 or 12 in Denali, an average of two days later in Denali (Table 16). This similarity in senescence dates supports the hypothesis that day length is a major factor in governing the end of the growing season.

The shortest growing seasons in both plots occurred in 2008; 109 days in the Copper Center Plot and 105 days in Denali Plot 2 (Figure 4). The longest growing season was 122 days in 2009 in Copper Center (Figure 4). The growing season length varied from 109 days to 122 days in Copper Center and 105 days to 114 days in Denali Plot 2 during these three years. This means that the growing season length varied between 8% and 11%. This is less dramatic than the variation observed in the two Denali plots that have been studied for six years and would likely increase with additional years of observation.

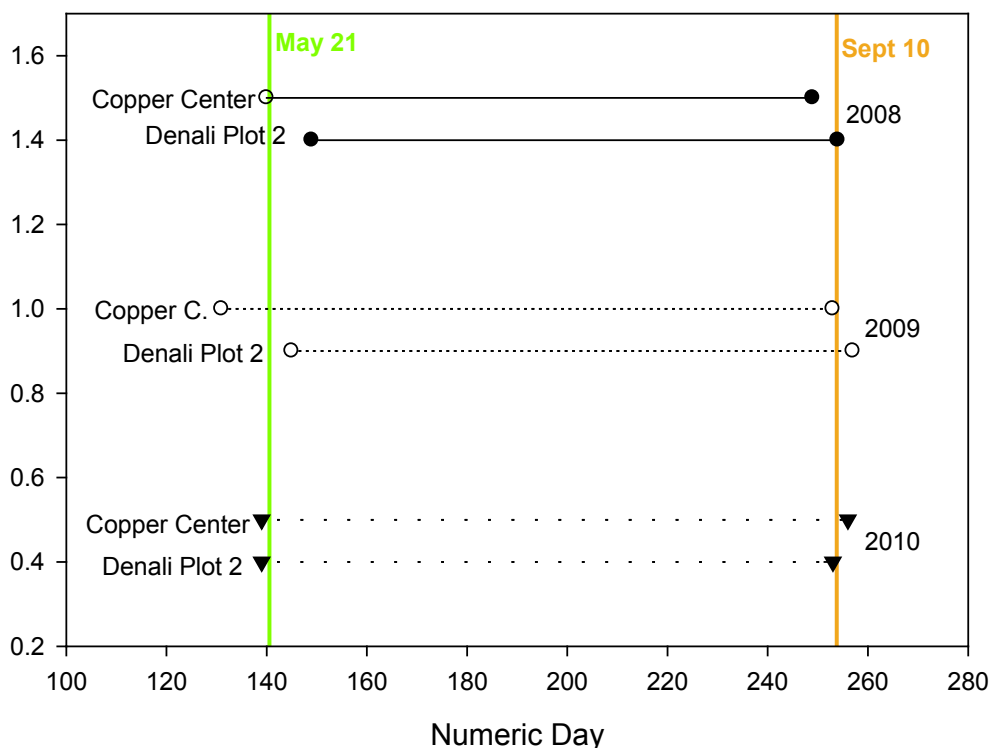


Figure 5. A schematic showing the estimated mean aspen growing season lengths for aspen phenology monitoring stations in Copper Center and Denali Plot 2 for the years 2008-2010. Vertical lines denote the average date of the start (green) and end (orange) of the growing season for the Copper Center and Denali Plot 2 over the years 2008-2010.

3.3.4 Variation in climate variables between the Copper Center Plot and the Denali Plot 2

The early growing season temperature in the Copper Center area was on average slightly warmer (by 3° C in April and 2° C in May) than the Denali Park Headquarters for the years 2008 to 2010. The snow free day at the two plots, however, was generally similar, averaging around May 5 or 6 (Table 15; note that the snow free date in the table is the actual snow free day in the plot). Only in Denali in 2008 did the snow hang around until the late date of May 12. The mean April temperatures were above freezing in all three years in Copper Center and below freezing for all three years in Denali (Table 15). Similarly, the mean May temperatures averaged two degrees warmer in Gulkana (8.55° C) than in Denali (6.46° C) and the sum of the thawing degree days was 66 degrees greater in Gulkana than Denali during the three years of concurrent observations (Table 16). The mean May temperature before bud burst was generally between four and six

degrees in the both plots (Table 15). The average of all three years of May temperature before bud burst was 2.44 ° C higher in Copper Center than in Denali; the driving force in this difference, however, were a couple extremely warm days in early May of 2009 in the Copper River valley. When we examine the mean May temperature before the start of the growing season, however, the differences are much reduced between the two areas with a three-year mean of 6.94° C in Gulkana and 7.12° C in Denali. It could be that this represents the approximate temperature needed for leaves to unfurl. May soil temperatures at the Copper Center Plot averaged 0.53° C warmer than the May soil temperatures at the Denali Plot 2 (Table 15). This difference is minor in comparison to the difference of 3.72° C that we observed between the Denali Plot 2 and Plot 1 for the six years of observations in Denali.

May of 2008 was cooler in both Gulkana and Denali than the average May temperature in the respective areas (for 2008, 2009 and 2010; Table 15), but Denali experienced several cold snaps during May that Gulkana did not. At the start of the month, mid-month and at the end of May mean daily temperatures were about four to six degrees colder in Denali than in Gulkana (Figure 6). These observations may play a part in explaining why bud burst and leaf unfurling was late in Copper Center and especially late in Denali during 2008. In Copper Center the first four days in May of 2009 were exceptionally warm, with temperatures above 9°C. In contrast, the temperature only rose above 9°C on one of the four warm days in early May in Denali (Figure 6). These hot, early temperatures in Gulkana may to some degree explain the extremely early bud burst in Copper Center during 2009 (Figure 6, Table 12). The mean May temperatures in Gulkana and Denali diverged less in 2010 than other years (1.59°C vs 2.15°C in 2009 and 2.52°C in 2008). This closer tracking of average daily temperatures coincides with the two plots having simultaneous leaf unfurling (though the dates of bud burst were still not the same in this year; Figure 6).

Table 15. Summary of selected early-season climate variables from the Copper Center Plot and the Denali Plot2. Climate data is from the Gulkana Airport for Copper Center and the Denali Park Headquarters (repeated from Table 10 for ease of comparison). Soil temperatures were taken at the phenology plots at the time of sampling. The snow-free day is when all the snow in the plot had melted.

Site-Year	Snow-free date at plot	Mean Air Temp:				Sum of thawing DD for May	Mean May soil temp in plot
		April	May	May 1- Bud Burst	May 1 to Growing Season Start		
CC-2008	May 5 (126)	0.37° C	7.55° C	5.74	6.43	234.6	0.94° C
CC-2009	May 5 (125)	0.69° C	8.98° C	10.40	7.65	268.9	0.31° C
CC-2010	May 5 (125)	1.1° C	9.11° C	5.85	6.75	299.0	0.43° C
CC-mean	May 5 (125)	0.47° C	8.55° C	7.33° C	6.94	267.5	0.56° C
DENA2-08	May 12 (133)	-3.85° C	5.03° C	4.91° C	5.10° C	158.06	-0.10° C
DENA2-09	May 4 (124)	-2.88° C	6.83° C	5.63° C	6.27° C	211.67	-0.43° C
DENA2-10	May 3 (123)	-1.10° C	7.52° C	4.12° C	4.89° C	235.28	0.61° C
DENA-avg	May 6 (127)	-2.61° C	6.46° C	4.89° C	7.12	201.67	0.03° C

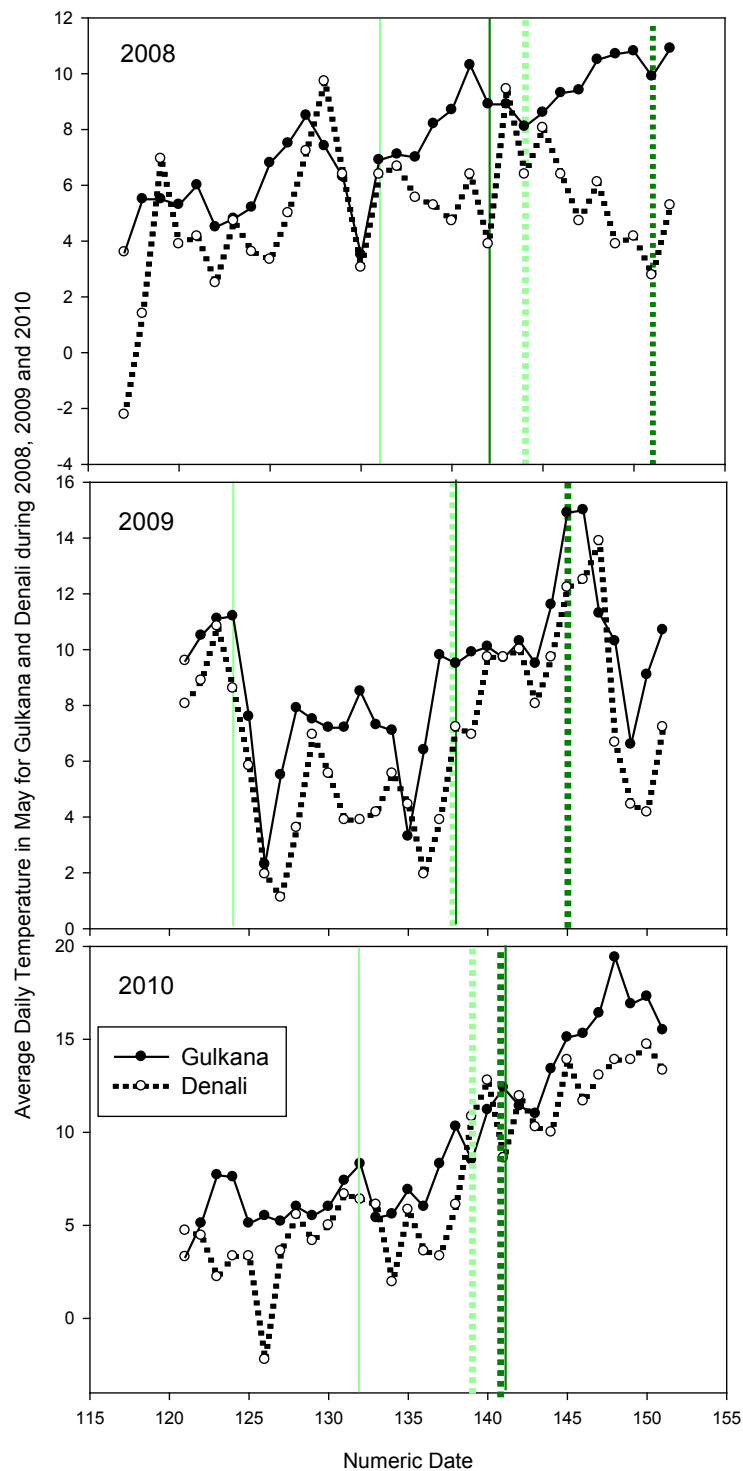


Figure 6. The graphs show the average daily mean temperature taken in Gulkana and Denali Headquarters. Vertical lines show the dates of bud burst and complete green-up: solid lines show the dates from the Copper Center Plot, while dotted lines show the dates for the Denali Plot 2. The light green vertical line shows the date of bud burst, while the dark green vertical line shows the date of complete green-up.

The temperature differences between Gulkana and Denali Headquarters in the fall followed a similar pattern as in the spring: mean daily temperatures and mean minimum temperatures were about one to one and a half degrees warmer in Gulkana than Denali and the two areas had more similar temperatures in 2010 than the other two years (Table 16 and Figure 7). Averaged over the three years, mean daily temperature between August 15 and September 15 was warmer in Gulkana than Denali by 1.07° C (Table 16). The mean minimum temperature was 1.49°C warmer in Gulkana than Denali (Table 16). The date that the temperature dropped below 2° C was identical in the two areas (Table 16 and Figure 7). Even the early cold snap on August 2, 2009 was experienced in both areas (Figure 7). On average the Gulkana Airport received 5.9 cm less of rain than Denali (Table 7). The difference in precipitation levels was greatest in 2008 with Denali Headquarters receiving 8.2 cm more of rain during the growing season than Gulkana, while the smallest difference in precipitation occurred during 2009 with Denali receiving only 2.9 cm more precipitation than Gulkana (Table 16). Precipitation readings at the RAWS weather stations (such as the one at the Gulkana Airport) are subject to some error and should be viewed with some caution.

The year 2010, during which temperatures in Gulkana and Denali tracked each other most closely, the difference in senescence timing between the two plots was not particularly reduced in comparison to the years during which the temperatures were more divergent (Table 16). This suggests that senescence is less dependent on temperature than is green-up, and potentially more dependent on other factors such as day length. In five of the six years of observations in Denali we observed that the first yellow leaves were seen within four days after the temperature dipped below 2° C. This appears to be less true in Copper Center where the temperature dropped below 2° C on August 9, 2008, but the ‘first yellow’ leaves were not observed until 9 days later (Table 16). Similarly in 2009, the first temperature to fall below 2° C occurred on August 10 (discounting the early cold snap on August 2), but the first yellow leaves did not occur until 16 days later (Figure 7).

Table 16. Summary of selected late-season climate variables from three years of phenology monitoring in Copper Center and Denali Plot 2 (DENA data repeated from Table 11 for ease of comparison).

Site-Year	Mean temp Aug1-Growing Season End	Mean Min. temp Aug1-Grow. Season End	Mean temp Aug 15 to Sept 15	Mean Min. temp Aug 15 to Sept 15	First date minimum daily temp. < 2° C	Total Precip. May 1 to Aug 31
CC-2008	10.56° C	5.46° C	10.05	5.45	Aug 9 (222;0.6°C)	17.5 cm
CC-2009	11.17° C	5.16° C	10.10	4.38	Aug 10 (222;0.6°C)*	14.7 cm
CC-2010	11.93° C	5.94° C	10.30	3.63	Aug 21(233;-1.1°C)	12.7 cm
mean	11.22° C	5.52° C	10.15	4.48	Aug. 13/14 (225.6)	15 cm
DENA2-08	9.15° C	2.69° C	8.95	2.59	Aug. 9 (222;1.67°C)	25.7 cm
DENA2-09	9.38° C	3.48° C	8.43	2.55	Aug.10 (222;1.1°C)*	17.6 cm
DENA2-10	11.17° C	5.61° C	9.85	3.84	Aug. 21 (233;1.7°C)	19.5 cm
mean	9.9° C	3.93° C	9.08	2.99	Aug. 13/14 (225.6)	20.9 cm

* A minimum temperature of 0° C in Denali and -1.1° C in Gulkana was reached on Aug 2, 2009, but this reading was considered too early in the season to impact senescence (Figure 3 and 16).

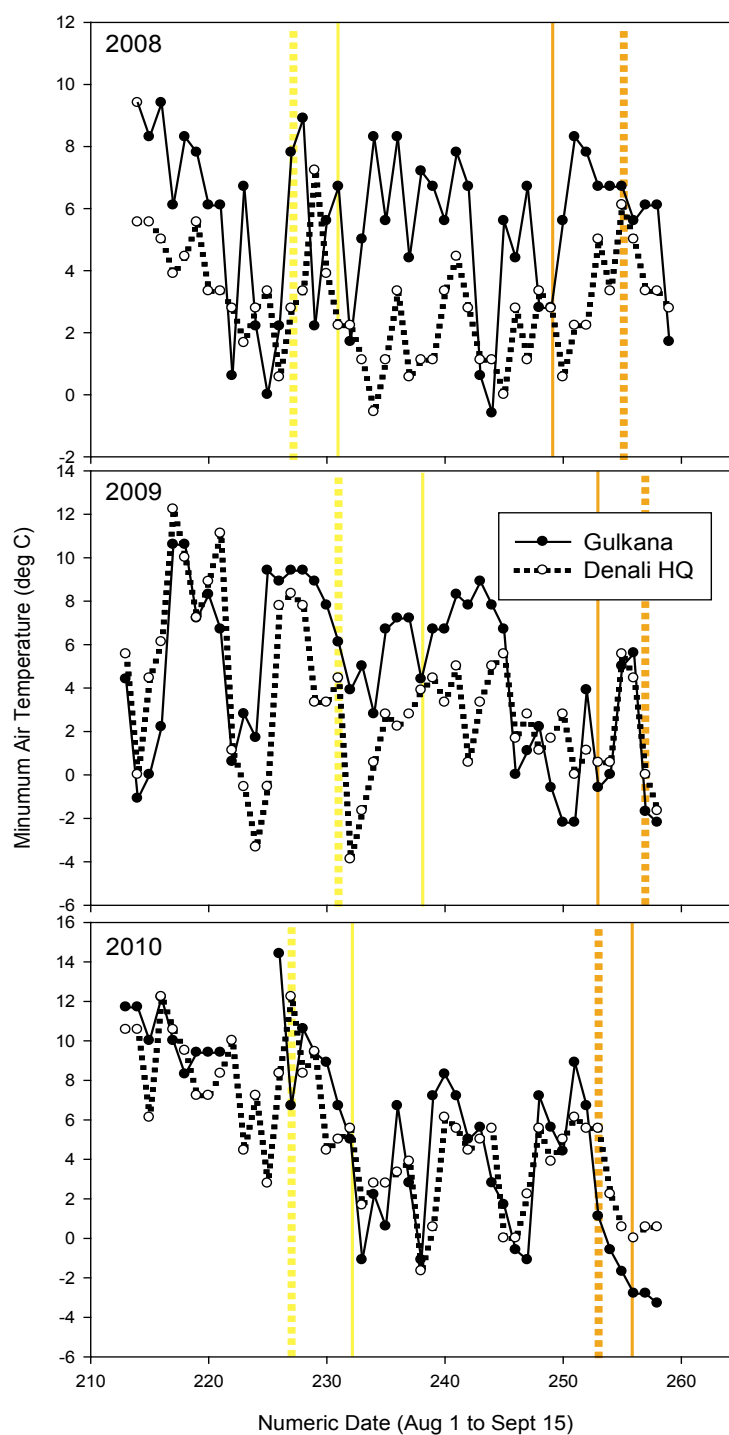


Figure 7. Three temperature plots showing the minimum daily temperatures recorded for the period Aug. 1– September 15, 2008, 2009 and 2010. Solid lines represent temperature data from the Gulkana Airport (~20km north of the Copper Center Aspen Plots) and dotted lines are temperature data from Denali Park Headquarters. The solid and dotted vertical lines indicate senescence benchmarks at the Copper Center Plot and Denali Plot 2 respectively, with the first vertical line of the pair (light yellow) showing the date the first tree with 25% yellow leaves was observed in a plot and the second line (orange) marking the date at which 100% of the trees in the plot had at least 50% yellow leaves.

3.3.5 Soil temperature

The mean sampling time soil temperatures were quite variable both from year to year and between plots. The Copper Center Plot generally had warmer soil temperatures than Denali Plot 2 (Figure 8), as was the case with mean air temperatures.

In 2008, both plots had soil temperatures near freezing on May 14 (day 135). Soil temperatures in 2008 warmed quickly in the Copper Center Plot to 2.7° C by June 4 (day 156), while soil temperatures rose comparatively slowly in the Denali Plot 2 reaching 0.9° C on June 4 (Figure 8). We observed the opposite pattern in 2009: on May 10 (day 130) the soil temperature was 0° C in the Copper Center Plot and -1° C in the Denali Plot 2.

In 2009 the soil temperatures rose slowly in the Copper Center plot reaching 0.6° C by May 20 (day 140) and rose relatively quickly in the Denali Plot reaching 0.98° C by May 27 (day 147; Figure 8). We do not have soil temperatures past May 20 in 2009 in the Copper Center Plot to directly compare to the Denali Plot 2 soil temperatures.

In 2010 the patterns in soil temperatures in the two plots were fairly synchronous: on May 5 (day 125) the soil temperature was -0.05° C in the Copper Center Plot and -0.17 in the Denali Plot 2 and by May 23 the soil temperatures were still fairly similar with 2.3° C in Copper Center and 1.9° C in Denali 2 (Figure 8). In both 2008 and 2009, when the soil (and air) temperatures from the Copper Center area differed more from the Denali Plot 2 temperatures the timing of leaf unfurling also differed. In contrast, when the temperatures in the two plots were more similar in 2010, the date of leaf unfurling was synchronous (Figure 8) suggesting temperature has a significant role to play in the timing of green-up.

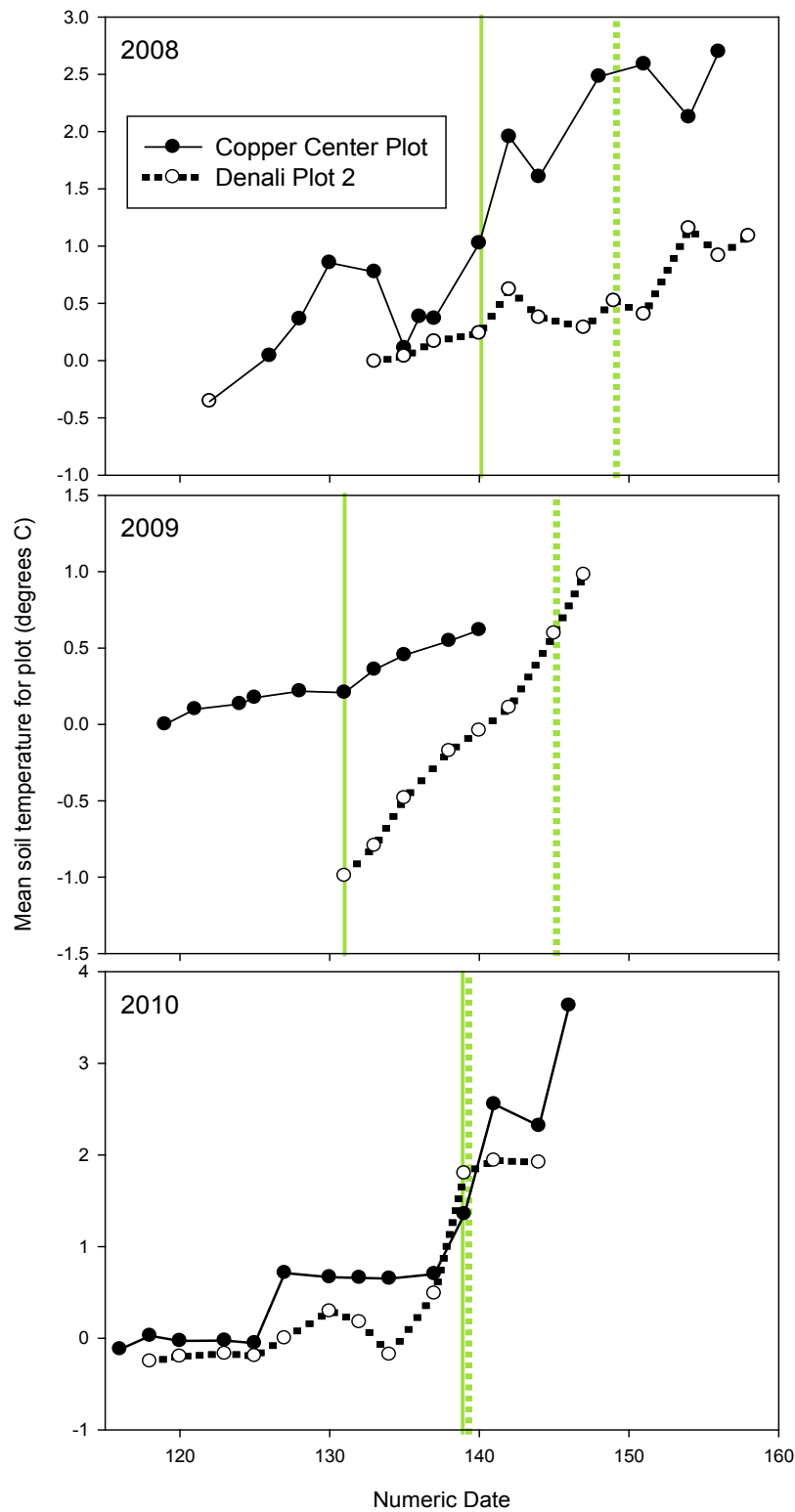


Figure 8. Graphs show the mean soil temperature taken at the time of phenology observation in the Copper Center Plot and the Denali Plot 2 during the years 2008, 2009 and 2010. Vertical lines indicate the start of the growing season, with solid lines representing Copper Center and dotted lines representing Denali Plot 2.

3.4 Relationships between Climate Variables and Aspen Phenology

In order to examine the relationships between phenology stages and climate variables we included data from the two Denali plots from six years, data from the Copper Center plot over three years as well as data from Eagle in 2008 and Fairbanks in 2010. This gives us a small sample size of 11. Though the results should be viewed with caution because of the limited years of observations, they may still give us general idea of what variables are important or not important in aspen phenology.

3.4.1 Relationship between Climate Variables and Spring Phenology Benchmarks

We calculated the coefficient of correlation for selected early-season climate variables and two spring green-up stages: bud burst and unfurled leaves. Overall, we found bud burst and leaf unfurling to have a weak correlation to the mean air temperature in April, but a strong correlation to climate variables related to mean May air temperature: as mean May temperature increases the date of bud burst occurs earlier (Table 17). Bud burst and complete green-up were most strongly correlated with mean air temperature during May and the sum of the thawing degree days in May (Table 17). The correlation between bud burst and mean May air temperature becomes weaker when only the days before bud burst or leaf unfurling are considered. This is counter-intuitive since clearly the temperature experienced by a tree after it has burst buds has no influence on when it experiences bud burst. This is likely explained by the influence of extremes when sample sizes are reduced. The number of data points contributing to the mean May temperature before bud burst is smaller than the 31 data points in the mean May temperature. Bud burst and unfurling dates were unrelated to mean May soil temperatures (Table 17). Warmer temperatures in the fall was modestly correlated with later bud burst (0.42) and the mean temperature during the previous fall had a modest positive correlation to later bud burst of 0.42, and positive correlation to later leaf unfurling (0.68; Table 17).

Table 17. Correlation coefficients between selected climate variables and two benchmarks of spring aspen phenology (n=17).

Climate Variable	Bud Burst Date*	Complete Green-up+
Snow-free date	0.69	0.70
Mean April Temp	-0.62	-0.60
Mean May Temp	-0.86	-0.85
Sum of Thawing DD in May	-0.84	-0.83
Sum of Thawing DD before unfurling date	-0.63	-0.80
Mean May Temp before bud burst date	-0.79	-0.56
Mean May Temp before unfurling date	-0.79	-0.64
Mean May Soil Temp (at time of sampling)	-0.12	-0.17
Mean Temp Aug 1 to growing season end (of prev year; n=12)	0.42	0.68

*Date by which at least half of the trees in the plots had burst buds

+Date by which 100% of the trees in the plots had unfurled leaves

3.4.2 Relationship between Climate Variables and Fall Phenology Benchmarks

The onset of senescence is most strongly correlated with the date of the first minimum temperature below 2°C (Table 18). It is also correlated with both the mean and mean minimum temperature between August 1 and the end of the growing season. The end of the growing season is most strongly correlated with total precipitation between May and August: high precipitation means correlate with earlier ends to the growing season. The end of the growing season is also

mildly correlated with the mean and mean minimum temperature during August 15 to September 15, but not at all correlated with mean temperature August 1 to the end of the growing season or the first date with a minimum temperature below 2°C (Table 18). The fact that these two senescence benchmarks are correlated to very different climate variables suggest the onset of senescence and the progression of senescence are influenced by different climate variables and the process of senescence does not necessarily occur in a linear progression.

Table 18. Correlation coefficients between selected climate variables and two benchmarks of fall aspen phenology.

Climate Variable	First Yellow*	Growing Season End+
Total precipitation May – Aug	-0.14	-0.63
Mean Temp Aug 1 to growing season end	0.52	0.05
Mean Min Temp Aug 1 to growing season end	0.61	0.1
Mean Temp Aug 15 to Sept 15	0.48	0.34
Mean Min Temp Aug 15 to Sept 15	0.48	0.41
First date of minimum Temp below 2°C++	0.64	-0.1
Mean Temp 14 days before growing season end	0.33	0.16
Mean Min Temp 14 days before growing season end	0.48	0.13
Mean Soil Temp at time of observations (aug-sept)	0.15	-0.33

*Date of first tree in plot with at least 25% yellow leaves. + Date 100% of trees in plot with at least 50% yellow leaves.

++Excluding the early freeze in 2009 that occurred on Aug 2.

3.5 Individual Variation in the Number of Days between Full Flower and Bud Burst

We examined the variation in the number of days between full flower and bud burst for individual trees. Because flowering events were limited during our five years of observations, examining individual trees allows us to see differences that would be masked with the plot averages we used for other phenology stages. We examined the difference in individual trees among sites, individuals, years and tree gender. Overall, we found that the days between full flower and bud burst were highly variable between sites, years, male and female trees, and even among years for individual trees that flowered on multiple years. The fewest days between full flower and bud burst were zero. On one occasion buds burst three days prior to full flower (Tree 8 in Copper Center in 2008). The greatest number of days between full flower and bud burst was 30 (Tree 10 in Copper Center in 2010).

We averaged the days it took individual trees to progress from full flower to bud burst for each of the study plots (Figure 9). We found considerable variation between plots. The trees in the Fairbanks plot progressed from full flower to bud burst the quickest with an average time of 5.8 days. We also found the least variability in this measure in the trees at the Fairbanks plot. Note that we only have data from 2010 for Fairbanks, so with future flowering events we will likely see more variation in this measure. Trees in the YUCH and Denali Plot 2 took a similar number of days to progress from full flower to bud burst: 7.5 and 7.8 days respectively (Figure 9). The south facing Denali Plot 1 and the Copper Center Plot (WRST1) both took the longest time between full flower and bud burst: 11.2 and 16.0 days respectively (Figure 9). We found the greatest variation between this mean for trees in the Copper Center plot with a range from -3 to 30 days to progress from full flower to bud burst (Figure 9). This variation between plots could be due to climate differences in the areas or to differences in tree genotypes in the different plots.

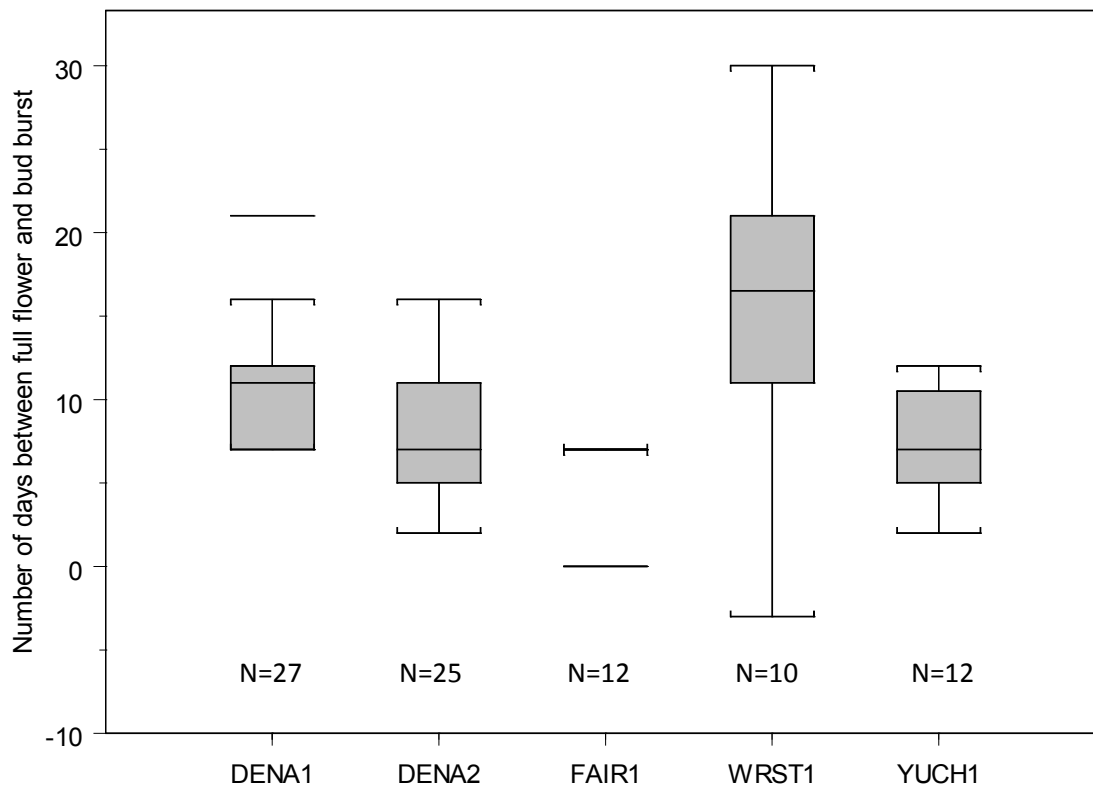


Figure 9. Box plot showing the range of variation in the days between full flower and bud burst. The sample size of individuals that flowered within each plot is shown below the box. If the number is greater than the number of trees in the plot, it is because some trees flowered in multiple years during our five-year observation period.

We also examined the variation in the number of days between full flower and bud burst among years. In 2006 no trees flowered. In 2009, only one tree in the Copper Center Plot flowered (Tree 8, which subsequently died that summer). We found the mean number of days between full flower and bud burst varied from 6.1 days in 2005, 9.8 days in 2006, and 10.7 days in 2010 (Figure 10). Both 2005 and 2010 had warm, dry spring weather, but both had quite different progression rates from full flower to bud burst. Years 2008 and 2010 had similar rates of progression and similar ranges of variability despite 2008 being particularly cool and 2010 being one of the warmer springs.

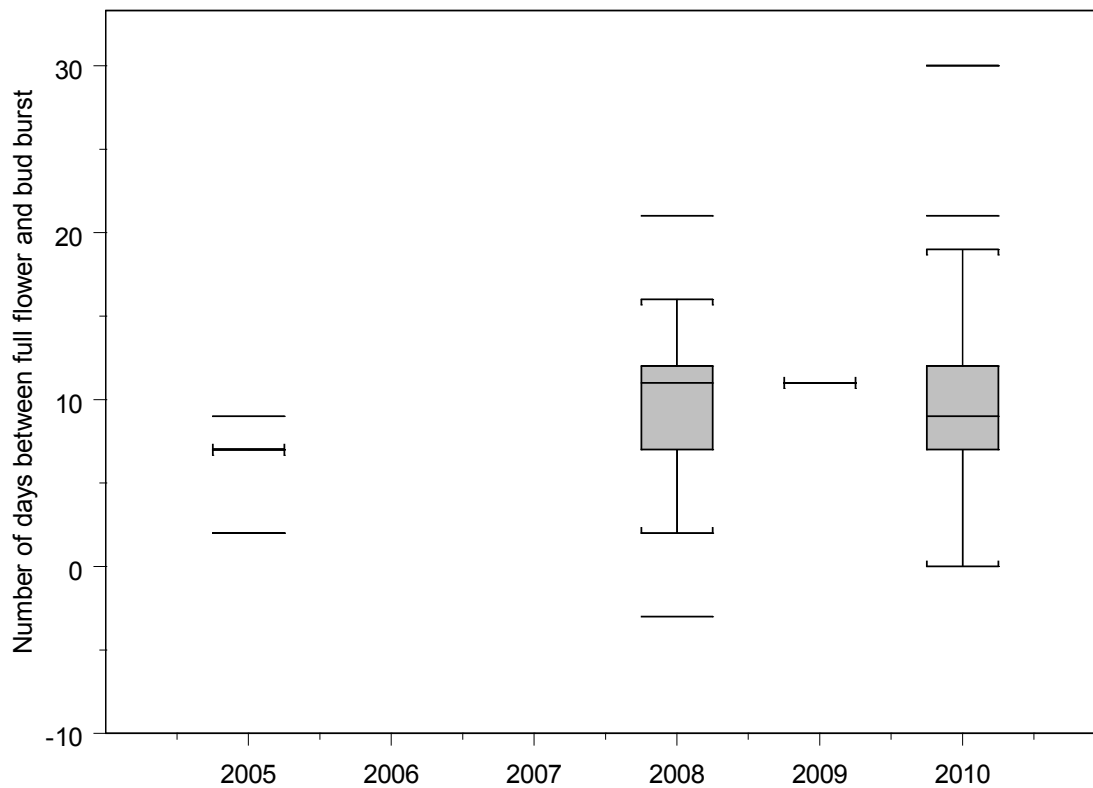


Figure 10. The number of days between full flower and bud burst among years. N=16 in 2005, N=25 in 2008, and N=41 in 2010. Data is taken from individual flowering trees from all sampled sites.

Several trees in the two Denali plots flowered on multiple years. We haphazardly chose several of the trees that flowered three times to determine whether they had a consistent number of days between full flower and bud burst or if they varied in this measure from year to year. We found no consistency within individual trees and high variation from year to year. For instance Tree 1 in Denali Plot 1 had only 7 days between full flower and bud burst in 2005, but then had 16 days in 2008 (Table 19). There appeared to be more consistency among years than within an individual across years (Table 19).

Table 19. The number of days between full flower and bud burst for individual trees in multiple years of flowering. Note that only a few of the trees that flowered on multiple years are shown as example of overall trend.

Tree ID (tree#/Plot)	Number of days between full flower and bud burst		
	2005	2008	2010
1/ DENA1	7	16	14
5/DENA1	7	11	9
9/DENA1	7	11	12
10/DENA2	2	5	7
3/DENA2	7	16	12
5/DENA2	7	12	5

For a subset of the trees that flowered, we have been able to determine the gender of the tree. In Denali Plot 1 we have three females and eight males, there is an even split in Denali Plot 2 and in Fairbanks there are seven female trees and five male trees, for a total female to male ratio of 15:18. Over the course of our observations we have seen 24 female and 37 male flowering events. We examined the variation the number of days between full flower and bud burst for the female and male flowering events. We found females more progressed consistently quickly from full flower to bud burst than males. On average it took female trees 7.25 days and male trees 10.03 days (Figure 11). Male trees tended to have a greater variation in the time between full flower and bud burst than female trees (Figure 11).

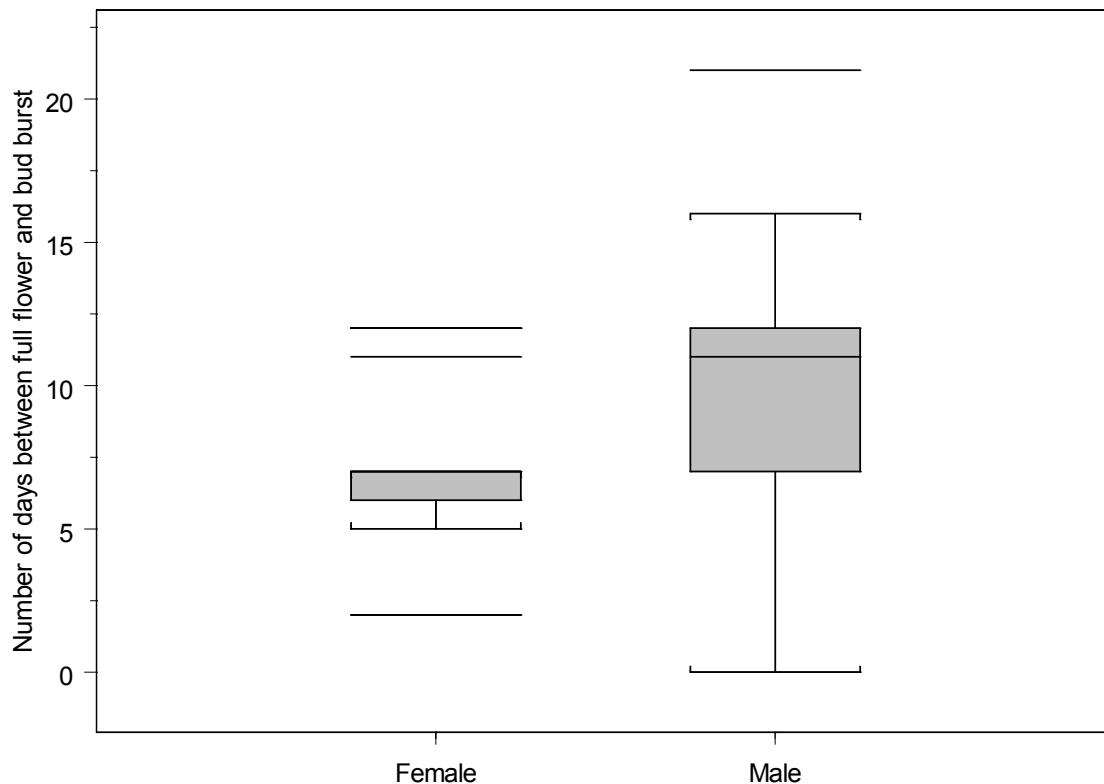


Figure 11. The number of days between full flower and bud burst for female and male trees in the Denali and Fairbanks aspen monitoring plots for the years 2005-2010.

4 Discussion

4.1 Bud burst and the growing season start

Our results suggest that out of the factors we measured, bud burst and complete green-up for our aspen trees was most strongly correlated with air temperatures and thawing degree days in May and had little correlation with soil temperature and potentially minimal correlation with day length. In warmer years in Denali, both plots had early bud burst and in colder years, both plots had delayed bud burst. Similarly, the Copper Center Plot, which had warmer spring temperatures than Denali on average, consistently had earlier bud bursts than Denali Plot 2. However, in 2010, when the temperatures in Denali and Copper Center were more similar, the two areas also had similar timing of bud burst. Such results are in agreement with studies investigating the trigger of spring bud burst in temperate, boreal and arctic ecosystems (Richardson and O’Keefe 2009).

Our results also suggest that bud burst and complete green-up was not correlated with soil temperatures and thus, not controlled by thawing of soil water. The two aspen phenology plots in Denali National Park were located in two very different habitat types: Plot 1 was in a steep, dry, south-facing area, while Plot 2 was in a flat, cool and moist location. We found that the soil temperatures in the spring time differed dramatically in these two plots, with average temperatures about 4°C warmer in Plot 1. Despite these differences, the two plots had nearly identical dates of green-up during our six years of observations.

We also found variation in bud burst from year to year. If day length was the sole controlling factor of bud burst, we would expect to find very consistent dates of bud burst from year to year. Though day length may still play a large role in influencing the timing of bud burst, our results suggest it is definitely not the sole controlling factor in green-up. Rather, May air temperatures, which are variable from year to year and likely increasing with climate warming, seem to play a large role in the timing of green-up, and thus, the growing season length and the amount of time a tree has to grow and reproduce. In fact, we found a 22% difference between the shortest and longest growing seasons in Denali. This large difference, mostly due to the differences in the timing of the growing season start, could have profound effects on the growth and reproduction of aspen trees from year to year. As climate changes over long time scales, a corresponding change in the start of the aspen growing season should be expected, and thus, potentially large scale changes in the amount of photosynthetic carbon gained by aspen trees.

4.2 Flowering

Flowering during the six years of our observations was sporadic. We had two years with no flowering at all, three years with minimal to moderate flowering and two years with a high percentage of trees flowering. These high flowering years appeared to be uniform across interior Alaska (we had high flowering in Denali, Fairbanks, and Copper Center in 2010). Wyckoff and Zasada (2008) cite that aspen produce some seeds almost every year and bumper crops on 3 to 5 year intervals. Wyckoff and Zasada (2008) also note that in a Wisconsin arboretum female trees flowered in 70% of the years observed and males flowered in 80% of the years. Our findings in interior Alaska are similar, but slightly lower percentage of year of flower: we saw flowering trees in 66% of the observation years (4 out of 6).

We found that the time between full flower and bud burst was different between female and male plants with female plants. Female plants tended to have less time between full flower and bud burst. This was primarily a result of earlier bud burst on the part of female plants (female had burst buds almost 4 days earlier than males) rather than earlier full flowering (female plants were in full flower just over a day earlier than male plants). Researchers have found that female aspen tend to have higher vegetative growth rates than male aspen (Grant and Mitton 1979). The shorter time between full flower and bud burst we observed in female aspen could be a result of or contribute to higher vegetative growth rates in females. If female leaf out earlier, they may have more time gaining photosynthetic carbon and thus have a higher growth rate. This difference in timing between female and male plants could also indicate a difference in the timing of resource allocation to growth and reproduction.

4.3 Leaf senescence and the growing season end

The timing of first yellow leaves and the end of the growing season had less obvious controlling factors than the start of the growing season. In general, mean fall air temperatures had little correlation to the timing of first yellow or the end of the growing season. We found that when spring air temperatures were warmer in Copper Center relative to Denali, we had earlier bud burst in Copper Center and when the spring temperatures in the area converged, we had more similar bud burst timing. We also found consistently warmer fall temperatures in Copper Center, but we did not find corresponding later senescence relative to Denali. The difference in the end of the growing season between the Copper Center Plot and Denali Plot two during the three years of concurrent observation was only 2 days. This suggests that mean air temperature in the fall has less influence on the timing of senescence than it does on the timing of green-up.

It also follows that other environmental factors play a role in the timing of senescence. These could be day length or access to water and nutrients. Averaged over the years of our observations, the two different Denali plots and the Copper Center Plot and Denali Plot 2 all reached 'first yellow' within 4 days of each other. This similarity between plots argues for a controlling factor, such as photoperiod, that is consistent across and plots at similar latitudes. We also found variation from year to year in the timing of 'first yellow', which indicates that more than just photoperiod is influencing the onset of senescence. With European Aspen, others have found photoperiod to control the onset of senescence and low temperatures to accelerate the process (Fracheboud et al. 2009).

We found the rate of progression from 'first yellow' to 'complete senescence' varied between the Copper Center Plot and the Denali Plot. Specifically, averaged over the three years of observations, the progression from 'first yellow' to all trees at least 50% yellow happens more quickly in the Copper Center Plot than the Denali Plot 2 (by 4.6 days on average), but that the progression from trees 50% yellow to complete senescence happens more quickly in Denali Plot 2 than in Copper Center (by 4.4 days on average; Table 14). Our results suggest there are different processes involved in senescence with potentially different environmental cues.

Our correlations between climate variables and fall phenology benchmarks indicate 'first yellow' and 'growing season end' are influenced by different climatic factors. 'First yellow' was most strongly correlated with the first minimum temperature below 2°C as well as mean minimum

temperatures between August 1 and the end of the growing season, while the 'growing season end' was most strongly correlated with rainfall. Higher rainfall rates corresponded to an earlier end of the growing season.

4.3 Summary

The timing of biological events is critical to the survival of a species, particularly in the far north where the winters are long and severe and the growing season is short. A plant has two strong conflicting incentives: 1) to avoid exposing valuable green leaves to freezing temperatures and 2) to maximize photosynthetic carbon gain. Understanding how plants resolve these conflicts is critical to understanding how plants will respond to changing climates. We have begun to study the phenology aspen trees in the parks of central Alaska. We are beginning to see what climate factors affect leaf out, flowering and senescence. Our initial findings suggest warming climate may correlate with earlier bud burst and thus a longer growing season, but that warmer temperatures may have less affect on the timing of senescence.

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