

## MORPHOLOGICAL AND PHYSIOLOGICAL PHENOLOGY OF *PINUS LONGAEOVA* IN THE WHITE MOUNTAINS OF CALIFORNIA

CHRISTINE HALLMAN<sup>1\*</sup> and HOWARD ARNOTT<sup>2</sup>

<sup>1</sup>Northeastern State University, Department of Geography, Political Science, & Sociology, 609 North Grand Avenue, Tahlequah, OK, 74464, USA

<sup>2</sup>Department of Biology, University of Texas – Arlington, 501 Nedderman St., Arlington, TX, 76019, USA

### ABSTRACT

Natural variations and responses to climate change can be identified within climatically sensitive ecosystems by monitoring growing season events. In 1962–1964, Fritts conducted a phenologic study on *Pinus longaeva* in the White Mountains of California. He monitored growing season events, environmental data, and dendrometer readings. In this study morphological and physiological phenophases, dendrometer traces, and environmental data were collected throughout the summers of 2007 and 2008 in the White Mountains of California to better understand variability in *Pinus longaeva* phenology and identify any shifts in the growing season since the 1962–1964 study (Fritts 1969). As a result of a late-season snow storm, observable phenophases in 2008 were 12 days later than in 2007. Pollination onset was slightly earlier than in the 1962–1964, which may indicate that accumulated heat or a combination of environmental factors influence these phenophases. Duration and timing of cambial activity in the present study was similar to that recorded in the Fritts (1969) investigation despite a median summer temperature increase of at least 2°C.

*Keywords:* bristlecone pine, cambial growth, phenology variability.

### INTRODUCTION

Tree species are unique in that their response to environmental conditions can be used as a fingerprint of climate change (Parmesan and Yohe 2003; Root *et al.* 2003) and represent a natural archive of past climate (Fritts 1976). Phenology, the study of periodic life cycle events, is influenced by seasonal variations in temperature and precipitation. Phenology is used to track ecological responses to climate variability and climate change (Walther *et al.* 2002). Identifying high-elevation conifer growing-season variability is crucial for recognizing deviations outside the normal growing-season range. This allows the recognition of shifts or changes in the growing season that are unprecedented and may be related to changing climate.

Starting in 1962, H.C. Fritts undertook a pioneering phenologic study on *Pinus longaeva* in the White Mountains, California. Growing season

events, a variety of environmental data, and dendrometer readings were collected during the summers of 1962, 1963, and 1964. His investigations provided both methodological standards, and comparison phenological data for this and future studies. With modern technology and photography, 45 years later this investigation reconstructs and extends the Fritts (1969) study to better understand the variability in *Pinus longaeva* morphological and physiological phenology and how individual phenophases are related to each other.

The objectives of this investigation were to answer the following: (1) what is the relationship between morphological phenophases, such as bud opening, pollination, and cambial activity? and (2) how does present bristlecone pine phenology compare to that observed 45 years ago by Fritts (1969)?

### PHENOLOGY

Observable phenophases in conifers include bud opening, needle elongation, emergence of

\*Corresponding author: hallman@nsuok.edu; Telephone: +918-444-3528; Fax: +918-458-2390

reproductive parts, pollination, and onset and cessation of cambial growth. The timing of morphological events (*i.e.* budburst, needle emergence) varies according to both genetic and environmental conditions (Dougherty *et al.* 1994; Chuine and Cour 1999; Cleland *et al.* 2007). In some conifer species, needle elongation takes place at the same time as branch elongation and appears to be influenced by temperature, water stress, and genetics (Dougherty *et al.* 1994). Physiological phenology refers to xylogenesis or the process of ring formation, including onset and termination of cambial growth. Growth onset is driven predominantly by spring temperatures (Rossi *et al.* 2007; Deslauriers *et al.* 2008). Cessation of growth occurs at approximately the same time annually, which suggests that photoperiod may control cambial growth termination (Dougherty *et al.* 1994; Rossi *et al.* 2006).

The timing of growing season events affects a variety of environmental processes. The initiation, ending, and length of the growing season influence global biogeochemical cycling by impacting movement and storage of water, carbon, and nutrients (Ludeke *et al.* 1994; Leinonen and Kramer 2002; Linderholm 2006). Additionally, accurate and precise phenological data have been indispensable for tree growth, climate, and ecological models used to better understand vegetation changes, which is key for identifying current tree-climate relationships and forecasting potential changes in forest growth, ecosystem productivity, and changes in carbon sequestration (Leinonen and Kramer 2002; Vaganov *et al.* 2005; Linkosalo *et al.* 2006; Cleland *et al.* 2007).

## **PINUS LONGAEVA AND PRIOR PHYSIOLOGICAL STUDIES**

*Pinus longaeva* (Great Basin bristlecone pine) are the longest-lived, annually dated trees in the world with the oldest at 4700+ years (Schulman 1958). Remnant bristlecone pine specimens remain on steep slopes in the White Mountains, California, for thousands of years (Ferguson 1968). As a result, multi-millennial length chronologies have been constructed from these samples in order to investigate past climate

conditions (LaMarche 1969; Hughes and Funkhouser 1998; Salzer *et al.* 2009).

Fritts (1969) conducted an intensive study of a variety of *Pinus longaeva* characteristics in the White Mts., CA. Of particular interest to the current study is the collection of phenologic and environmental data in the summers of 1962–1964. Growing season observations were recorded on several *Pinus longaeva* in Cardis Valley, which is located 1.8 km north of the Schulman Grove Visitor Center. According to the 1962–1964 study, bud swelling occurred in late June-early July and growth ceased after 45–56 days for young trees (100 to 300-years old) and 35–43 days for old trees (>600 years). Phenophases varied from year to year and with elevation. *Pinus longaeva* at high elevations began growing 10–12 days later than at low elevations. Onset of growth depended on temperature whereas rate of growth depended on moisture regimes.

The approach taken in this investigation involved studying *Pinus longaeva* phenology at Fritts' historic Cardis Valley field site in the White Mountains of California to document morphological and physiological phenophases (Figure 1). With growing-season data from Fritts (1969), the present study was able to identify and document *Pinus longaeva* phenophases for two years, as a rough assessment of changes over the past decades since Fritts' work (1969). Growing season and environmental information collected over 45 years ago in Cardis Valley (Fritts 1969) were compared with data from this study to gain insights on *Pinus longaeva* growth patterns.

## **METHODS AND MATERIALS**

### **Study Area**

Cardis Valley, located in the White Mountains, California (37°N, 118°W) *ca.* 18 km north-east of Bishop, California, runs east-west, has an elevation of 3200 m a.s.l., and is 1.8 km north of the Schulman Grove Visitor Center (Figure 1). The valley floor contains 15 to 30 cm of sandy soil while adjacent valley walls consist of Reed Dolomite gravel and cobbles with 10–30° slopes. The site receives only 20 cm of precipitation a year on average and experiences temperatures ranging



Figure 1. Historic Fritts (1969) phenology site in Cardis Valley.

from  $-22$  to  $30^{\circ}\text{C}$  annually (Hall 1991). Valley winds are highly variable with no predominant wind direction noted in summers 1962–1964 or 2007–2008. As observed in May 2008, Cardis Valley accumulates snow during the winter and spring. Field observations of damaged, bent, and leaning small-diameter trees in Cardis Valley indicate snow levels have reached 70 cm. The forest valley is open with no understory and the majority of trees are *Pinus longaeva* with a small population of *Pinus flexilis*. The site contains a few strip-bark trees, but most are full-bark straight-bole trees. Strip-bark bristlecone pines exhibit cambial dieback as a result of root exposure, damage, desiccation, and/or scouring by wind and soil (Brunstein 2006). The remaining vegetation consists of annual herbaceous dicots and small trees of *Cercocarpus* or Mountain Mahogany. Char on trees indicates the area has been burned in the past, but no fire history studies have been conducted in this area. The nearest climate station is White Mountain Research Station at Crooked Creek located 11 km north of Cardis Valley. The

location of this study site limits visitor interference, is relatively accessible, and enables the study of several *Pinus longaeva* in close proximity to each other (Fritts 1969).

### Data Collection and Methods

The original Fritts (1969) site was pinpointed based on the map published in the 1969 article. A photograph in the same article and identification of screws and putty on three trees verified that the location was utilized by Fritts (1969). Those same three trees were utilized in the present study along with trees in close proximity where lower branches were accessible for measurement.

The present phenological study included 16 trees in 2007 and 2008 and five additional trees in 2008. All but three of the study trees grow on the valley floor; two are located on the south-facing slope and the other on the north facing slope of adjacent valley sites. North and south-facing branches were chosen where available to examine terminal bud diameter and length and needle length.

Morphological phenophases based on reconstructed Fritts (1969) descriptions were identified and documented during the summers of 2007 and 2008 (Figure 2). These phenophases were recorded via photographs and measurements taken every 3 to 4 days from four branches per tree. Bud diameter and length were measured so that more precise data could be collected to describe bud swelling and elongation. Additionally, in 2008, USA-National Phenology Network protocols (<http://www.usanpn.org/>) for needle emergence and first pollen shedding were utilized.

Cambial samples were collected weekly in the summers of 2007 and 2008 from five trees each summer. Cambial plugs contain the bark, cambial zone, and the outside 3–7 rings, thereby allowing the identification of active tracheids and cambial activity. In this case, cambial activity refers to formation and life span of tracheids. Cambial punches were taken on various sides of the tree in order to lessen damage to one particular location on the tree stem (Fritts 1969). The five trees punched in 2008 were also equipped with point dendrometers (Gensler and Diaz-Munoz 1983). Dendrometers were placed near the base of the tree and cambial samples were taken 1–1.5 m above the ground to reduce the likelihood of increased growth resulting from cambial injury caused by dendrometer installation (Fritts 1969). Cambial samples were stored in Formalin-Acetic Acid-Alcohol (FAA) solution, 70% alcohol (Arnott 1958) in the field and were processed by Dr. Howard Arnott. Samples were thin-sectioned using razor blades, and active tracheids were counted (Bonar *et al.* 1925; Foster 1942; Sass 1951; Berlyn and Miksche 1976). These procedures were similar to those in Fritts (1969). The progressive pattern of *Pinus longaeva* ring formation is documented in Figure 3.

Morphological phenophases were compiled and dates were determined for each tree based on the average of four observation branches. Morphological and cambial phenology dates for 1962–1964 were compared statistically with those collected in this study; where observations from multiple trees existed from Fritts (1969), paired two-sided t-tests were used to identify any significant differences between the 1962–1964

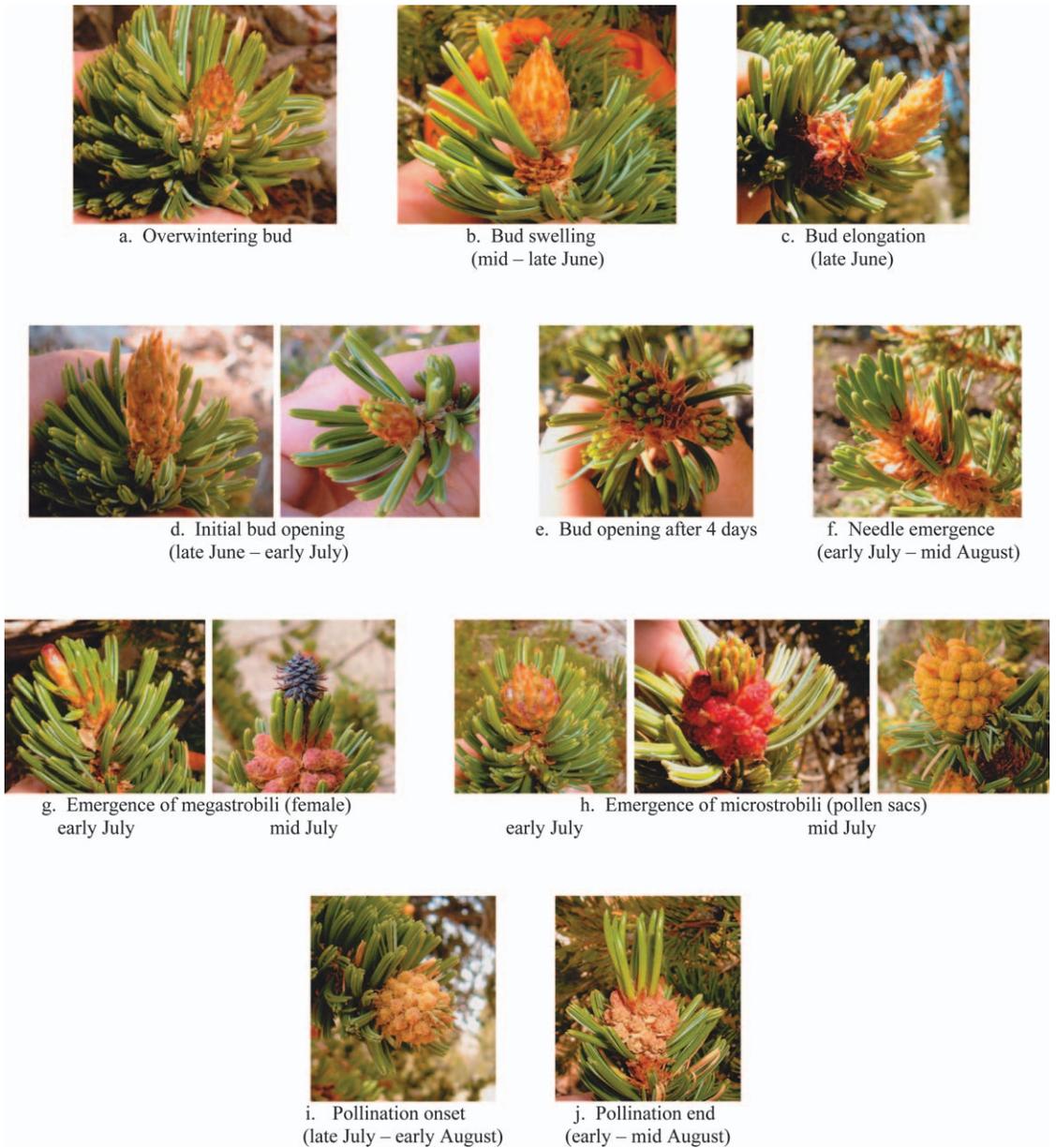
study and this investigation (Kleinbaum *et al.* 1988). In cases when only a mean was given in Fritts (1969), the means were compared using a one-sided t-test. To identify any relationships between phenophases, weekly rates for bud swelling and elongation, needle elongation, and tracheid formation were calculated and analyzed.

A variety of environmental data were also collected at Cardis Valley. Two DS1921G thermochron sensors (Maxim, California) were installed on two trees at heights of 1.5 to 3 m and read temperature every 4 hours. A weather station was set up during the observation period with a S-LIA-M003 photosynthetically active radiation sensor, a S-WCA-M003 anemometer, and a TMC20-HD soil temperature sensor at a depth of 15 cm recording every 30 minutes on a HOBO® datalogger (Onset, Massachusetts). An analog rain gauge at a height of 1.4 m was installed and checked every 3 to 4 days throughout the summers of 2007 and 2008. Daily averages for minimum and maximum air and soil temperatures were calculated.

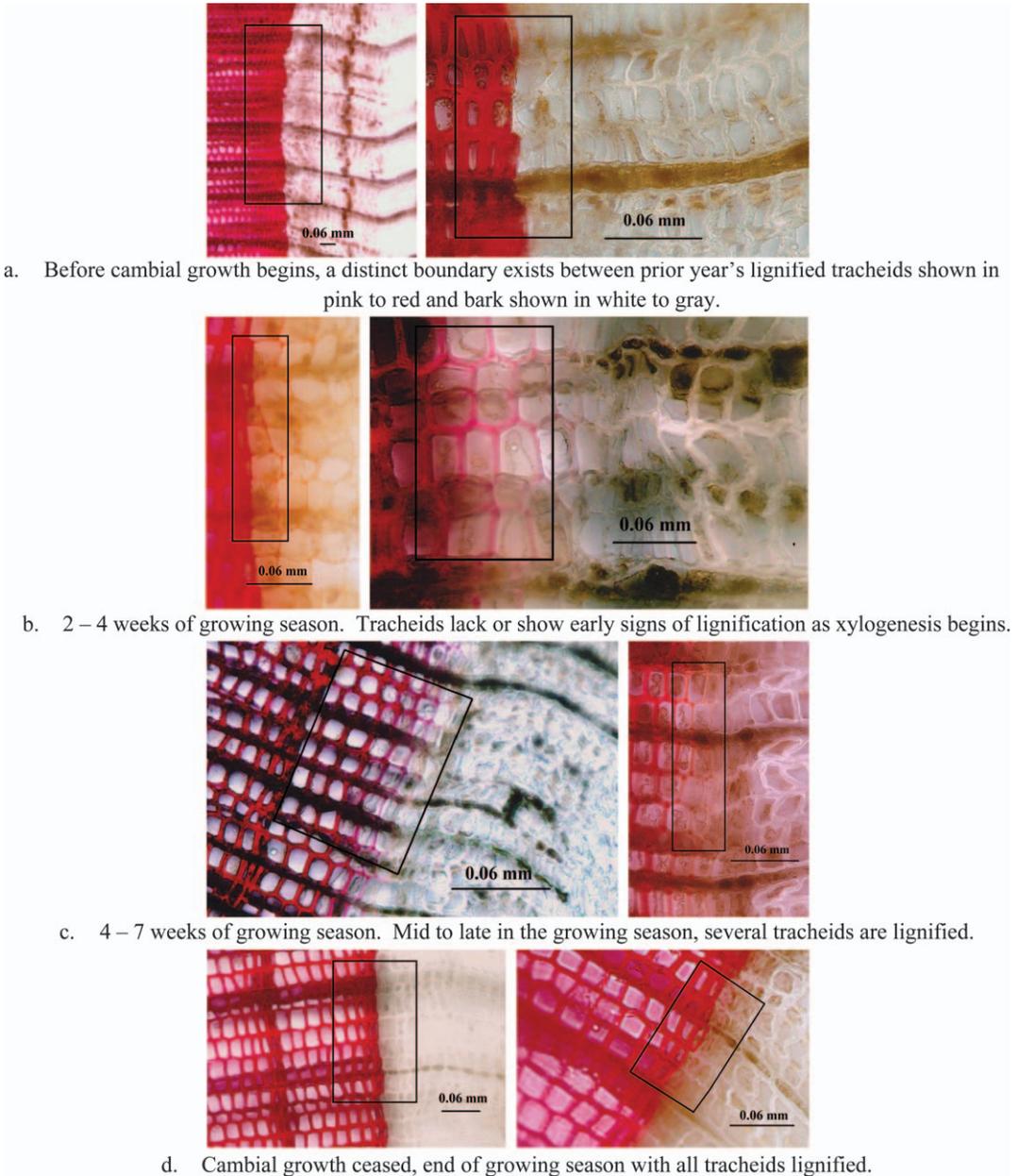
## PHENOLOGY OBSERVATIONS AND RESULTS

Phenological observations indicate that growing seasons in 2007 and 2008 were of similar length and that phenophases progressed in the same sequence. However, variability in the timing of phenophases was observed. Bud swelling, elongation, opening, and pollination were more variable in 2008 than 2007. The majority of physiological and morphological phenology occurred earlier in 2007 than 2008 (Figure 4 and Table 1). Dates associated with the first appearance of reproductive parts were similar in both years. The period of pollen shedding was longer in 2008, probably because more male cones were produced in that year. Peak photosynthetically active radiation was similar for both seasons (*ca.* 2500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), and soil temperature variability mimicked air temperature. No patterns between wind measurements and growing season events were identified.

Cambial growth data show some similarities and some differences between the two years. In 2007 and 2008, cambial onset initiated during bud



**Figure 2.** Phenologic photographic diary. Pictures taken summer 2007 and 2008. Sequence begins with an overwintering bud (a), then progresses to bud swelling (b) where bud scales pull away from bud (measured diameter). Next, the bud elongates (c) with a pronounced lengthening (measured length). Initial bud opening is defined as the opening at the tip of bud where tips of needles are visible (d). This phenophase is the same as the USA-National Phenology Network emerging needles stage. After four days, tips of needles separate, and the bud for next year is visible (e). Needles continue to emerge and separate throughout the growing season (measured length) (f). Beginning to emerge from the bud is a megastrobilus and a fully emerged female cone is seen about a week later (g). Megastrobili vary from blue to purple. Microstrobili or “pollen sacs” appear at the base of the bud and vary from yellow to red (h). Reproductive parts tend to appear simultaneously on various branches of a tree. Pollination onset (i) occurs when pollen first sheds from a shaken branch whereas pollination end (j) occurs when pollen does not fall when a branch is shaken. *Pinus longaeva* sheds yellow pollen except for one known instance where pollen is white. Pollination onset is the same as the first pollen shedding stage in USA-NPN standards. Note in this and the Fritts studies that measurements were obtained using four designated branches per tree although USA-NPN standards use three locations on a tree for phenophase determinations.

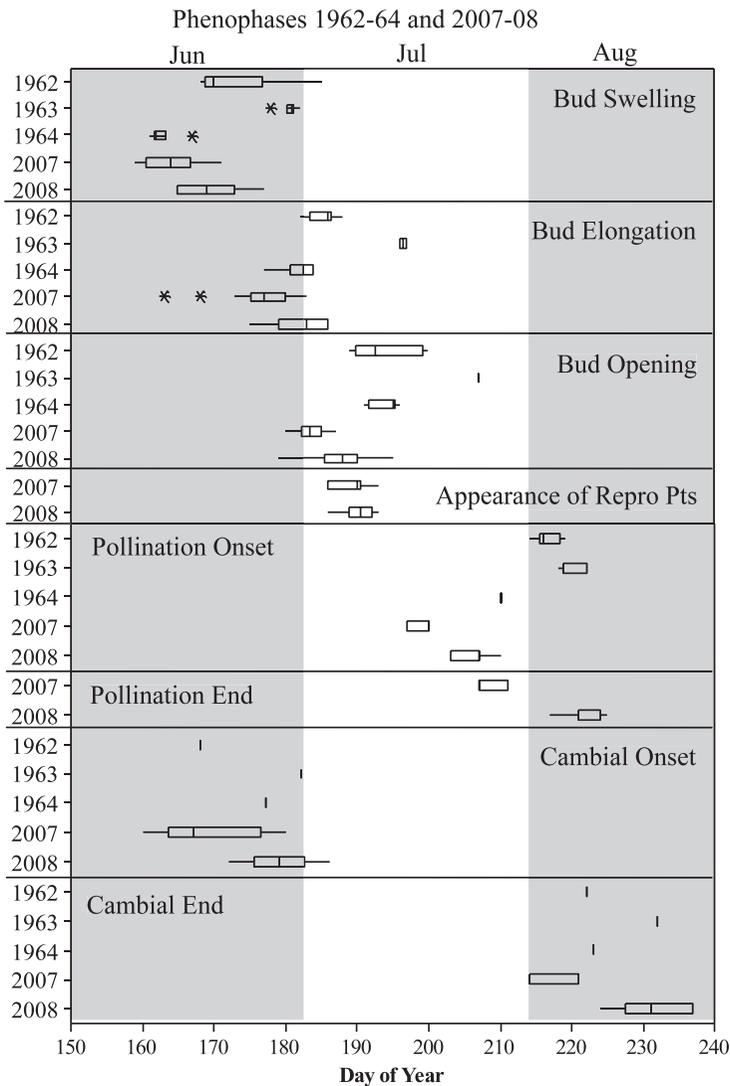


**Figure 3.** Cambial growth in 2007 and 2008. a. Before cambial growth begins, a distinct boundary exists between prior year's lignified tracheids shown in pink to red and bark shown in white to gray. b. 2–4 weeks of growing season. Tracheids lack or show early signs of lignification as xylogenesis begins. c. 4–7 weeks of growing season. Mid to late in the growing season, several tracheids are lignified. d. Cambial growth ceased, end of growing season with all tracheids lignified.

swelling and elongation whereas bud opening occurred soon after cambial activity began (Figure 4). Generally, pollination ceased before cambial activity ended. The length of cambial activity was virtually the same in 2007 and 2008

whereas the timing of growing season onset was shifted 12 days later in 2008 probably as a result of the aforementioned late season snow storm.

A comparison of results from this study and Fritts (1969) show that cambial activity



**Figure 4.** Box plots for 1962–1964 and 2007–2008 phenophases. Appearance of reproductive parts and pollination end were only available for 2007–2008 seasons. Cambial onset and end for 1962–1964 were measured by Fritts (1969), but only available as an average. Stars represent outliers.

during the 1962–1964 study varied from 46 to 54 days in length, which is similar to both 2007 and 2008. Bud opening in 2007 was earlier than 1963 and 1964 whereas 2008 bud swelling, elongation, and opening were earlier than 1963 data (t-test,  $p < 0.01$ ) (Table 2). Bud swelling and elongation in 2007 was noticeably earlier than 1963. Pollination onset was earlier in 2007 and 2008 than in 1962–1964. 1962 cambial onset was 11 days earlier than 2008 whereas cambial end was much later in 1963 as opposed to 2007. Differences in the timing of

cambial onset between these two years appear to be associated with weather variability (Figure 5).

Relationships between cambial growth and phenophases were examined based on the weekly phenological observations and cambial activity determined from the punches. Mean weekly rates were calculated for bud diameter and length, needle length, and cambial activity so that relationships between phenophases could be identified (Figure 6). A slight decrease in rate of bud length growth coincided with cambial onset. A

**Table 1.** Phenological activity for 1962–1964 and 2007–2008. Cambial activity is an average. Mode given in parenthesis for bud opening, appearance of reproductive parts, onset of pollen shedding, and pollination duration. Bud swelling and elongation not included because they are difficult to reconstruct based on Fritts (1969).

Year	Cambial Activity (Total Length in Days)	Bud Opening	Appearance of Reproductive Parts	Onset of Pollination	Pollination Duration
1962	168 to 222 (54)	189 to 200 (190)	—	214 to 219 (216)	—
1963	182 to 232 (50)	207	—	218 to 222 (222)	—
1964	177 to 223 (46)	191 to 196 (195)	—	210	—
2007	167 to 221 (54)	173 to 190 (183)	186 to 197 (186)	197 to 200 (200)	197 to 211 (200 to 207)
2008	179 to 231 (52)	179 to 193 (186)	186 to 200 (189)	203 to 210 (207)	203 to 225 (207 to 224)

decrease in needle length occurred simultaneously with pollination end. A maximum in needle length growth occurred with cessation of cambial growth. In this case, cambial end represents the end of new tracheid formation.

Not surprisingly, rain events and cloud cover play a key role in stem growth variability, as indicated by dendrometer measurements over the two summers. Two rain events of more than 0.2 cm were recorded in the summer of 2007 whereas four were recorded in 2008. Abrupt increases in the dendrometer trace coincide fairly well with rain events (Figure 7). Bud swelling corresponds to a

small temporary increase in stem width, which does not coincide with a precipitation event. This may represent hydration of the stem after the dormant season (Turcutte *et al.* 2009).

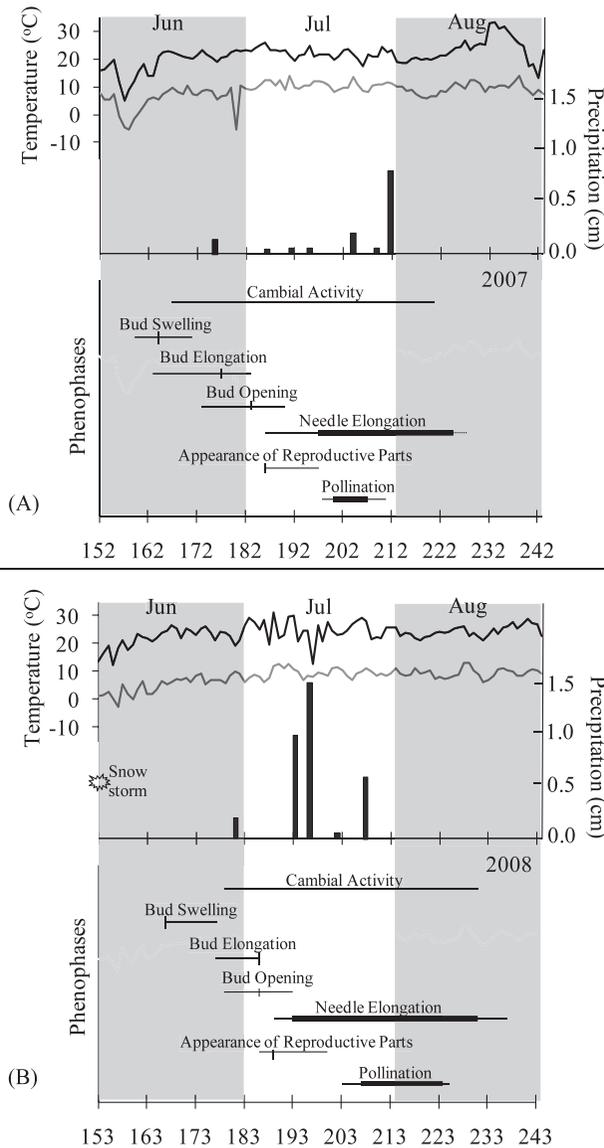
## DISCUSSION

Phenophase observations carried out over the summers of 2007 and 2008 indicate that growing season events progress in a predictable sequence whereas timing of events vary as a consequence of intra-annual differences in weather. In comparison with those observations made by Fritts (1969), growing season length is similar (*ca.* 50 days) whereas bud opening and pollination onset are earlier in the current study. Overall 2007 and 2008 cambial activity duration and timing are similar to Fritts (1969) and appear to be within normal documented variation; suggesting that slight differences are a result of natural variability.

This study indicates that the duration of cambial activity did not differ between the 1962–1964 and 2007–2008 studies whereas bud opening and pollination onset were earlier in 2007–2008 (Fritts 1969). Cambial activity for *Pinus longaeva* lasted 50 to 54 days with the exception of 1964 when it was 46 days. The shortening of cambial activity in 1964 may be associated with cooler springtime temperatures (Fritts 1969). Onset of pollen shedding in this investigation was statistically earlier than the Fritts study. Bud opening was earlier in 2007–2008, but was not significantly different from data collected in the 1960s. Earlier bud opening and pollination onset may be related to the impact of accumulated heat or more complex environmental factors that are influenced by increasing temperatures and do not affect cambial activity in the same way.

**Table 2.** Significance values for mean comparison between present study and Fritts (1969). \* = one sided t-test. Paired two-sided t-test used for all others. Values shaded are significant at  $p < 0.01$ , meaning for a given phenophase the two years are significantly different. No data for 1962–1964 are available for first appearance of reproductive parts or pollination end.

Phenophase	Fritts (1969)	2007	2008
Bud Swelling	1962	0.01	0.51
	1963	<0.00	<0.00
	1964	0.61	0.01
Bud Elongation	1962	0.01	0.90
	1963	<0.00	<0.00
	1964	0.12	0.05
Bud Opening	1962	0.01	0.39
	1963*	<0.00	<0.00
Pollen Shedding Onset	1964	<0.00	0.01
	1962	<0.00	<0.00
Cambial Onset	1963	<0.00	<0.00
	1964*	<0.00	<0.00
	1962*	0.70	<0.00
Cambial Cessation	1963*	0.02	0.25
	1964*	0.09	0.42
	1962*	0.04	0.01
	1963*	<0.00	1.00
	1964*	0.02	0.02

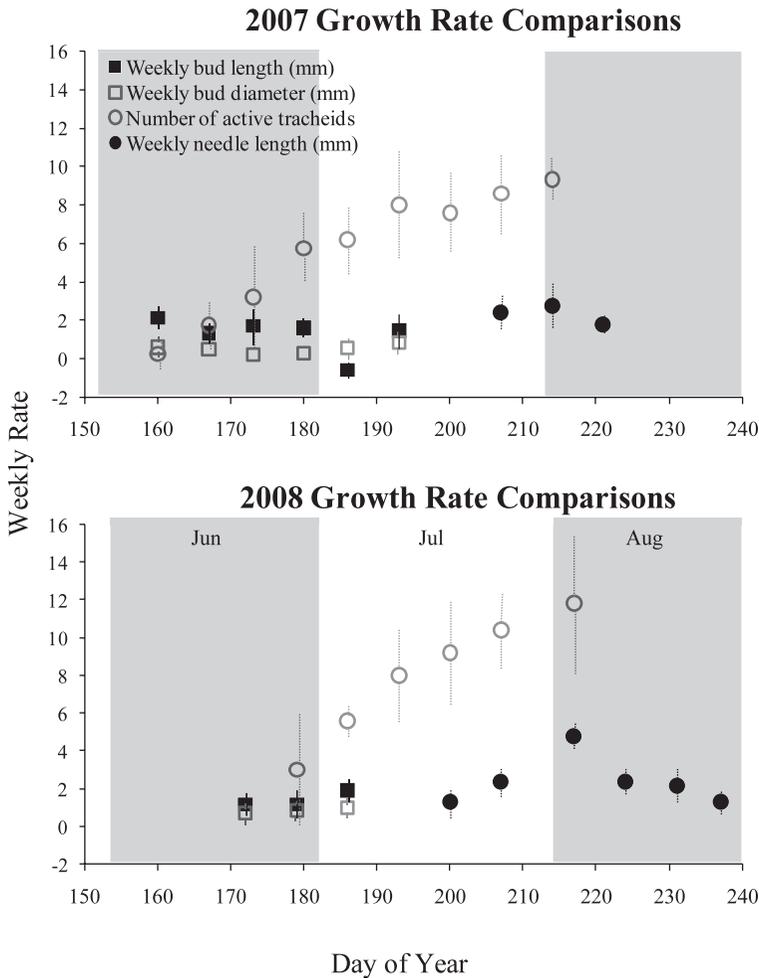


**Figure 5.** June–August 2007 (A) and 2008 (B) temperature, precipitation, and phenophases. Horizontal scale in Day of Year. Vertical line = mode. Wider line on needle elongation and pollination = mode.

Several studies show growing-season shifts and/or elongation in some regions associated with climate change (Cleland *et al.* 2007; Schwartz *et al.* 2006; Walther *et al.* 2002). The entire *Pinus longaeva* growing season does not appear to be shifting or lengthening at this location, but particular phenophases occurred earlier in the present study. This suggests that increasing temperatures may be affecting specific *Pinus longaeva*

growing-season events, particularly pollination onset. In order to eliminate the possibility that differences in observation frequency led to a discrepancy in bud opening and pollination onset dates between the 1962–1964 investigation and this work, further study is necessary.

According to data collected at the Fritts site in the 1962–1964 study, maximum air temperatures rarely reached 20°C with average maximum



**Figure 6.** Comparison of growth rates.

and minimum temperatures of *ca.* 13–17°C and 8–10°C, respectively (Fritts 1969). On the other hand, average maximum temperatures for 2007 and 2008 ranged from 21.3 to 23.7°C with average minimums reaching 8.6 to 7.9°C, respectively. In order to confirm average temperatures during the summers of 1962–1964 and 2007–2008, data from a nearby weather station, Crooked Creek, were utilized for comparison (WMRS, accessed 5 March 2010). Consistent with the present study, average June–August temperatures are at least 2°C warmer in 2007 and 2008 than 1962–1964. In spite of the warmer temperatures, the timing and duration of cambial activity was fairly constant between the two studies, suggesting that in regards

to xylogenesis, non-treeline *Pinus longaeva* at 3200 m has not changed in response to increasing temperature. On the other hand, onset of pollination may be occurring earlier, and potentially altering reproductive cycles of these ancient trees. Only continuous data collection can reveal long-term trends in these phenologic changes.

Data recorded in 1962–1964 and 2007–2008 imply that onset of cambial growth and bud opening occur earlier in warmer, drier springs (Figure 4). This is substantiated by conifer studies indicating that earlier onset of cell production is associated with warm springs (Deslauriers *et al.* 2008). Observations involving high-elevation *Pinus monticola* and *Abies magnifica* found in the

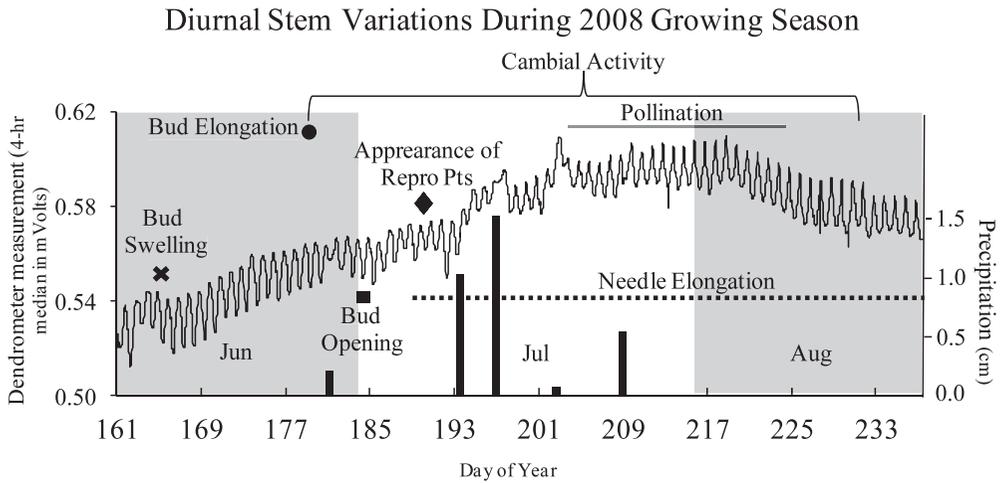


Figure 7. Median Point Potentiometer Dendrometer summer 2008. Precipitation in vertical bars.

Sierra Nevada, California suggest that snowmelt and no-snow dates influence onset of stem growth (Royce and Barbour 2001). With early snow melt, warm spring temperatures, and/or no late spring snowfall, onset of cambial activity and bud opening tend to occur early as opposed to years when spring temperatures are cool and snow cover is present. Therefore, if spring months in the White Mountains are warm and dry over an extended period of time, changes in the timing of phenophases may occur.

**CONCLUSIONS**

This research provides an updated and detailed examination of the growing season of *Pinus longaeva* in the White Mts., California. As in Fritts (1969), phenophases occur in a sequential pattern driven by genetics. Cambial onset varied by twelve days in 2007 and 2008 as a result of intra-annual weather variations whereas the duration of cambial activity was nearly the same for both years. The duration of cambial activity for this study and Fritts (1969) are similar except for 1964, in which the growing season was slightly shorter. Onset of pollination was significantly earlier in 2007–2008, which may be a response to increasing temperature. This study and Fritts (1969) found that earlier growing season onsets tend to occur in dry, warm springs, suggesting that during extended dry, warm periods, shifts to earlier growing season onsets may occur.

Two short periods of time, 1962–1964 and 2007–2008, do not provide adequate data to identify long-term phenologic patterns, but rather they simply present data on the possible natural range of growing season variability. Frequent monitoring of phenology will reveal long-term growing season trends in these and other climatically sensitive trees.

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