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Internal temperature of Douglas-fir buds is altered at elevated temperature[☆]

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Abstract

Pseudotsuga menziesii (Douglas-fir) saplings were grown in sun-lit controlled environment chambers at ambient or elevated (+4°C above ambient) temperature. We measured internal temperatures of vegetative buds with thermocouple probes and compared temperatures of normal buds and abnormal buds with loosened, rosetted outer scales in elevated temperature chambers. The abnormal buds had higher and earlier peak daily temperatures than normal buds. Elevated temperature may influence the internal temperature of buds and contribute to the development of abnormal, rosetted buds with loosened outer scales. Abnormal bud development may alter branching patterns and allometry of Douglas-fir trees subjected to climatic change. Published by Elsevier Science B.V.

Keywords: Bud; Climate; Douglas-fir; Morphology; *Pseudotsuga menziesii*; Temperature

1. Introduction

Elevations in temperature associated with predicted changes in climate may influence the development of forest trees (Dale and Franklin, 1989; Billington and Pelham, 1991), as in the case of Douglas-fir saplings, which were reduced in height (Olszyk et al., 1998) and which had abnormal buds with loosened and reflexed (rosetted) outer scales at elevated temperature (Apple et al., 1998). As buds are the points of needle and branch

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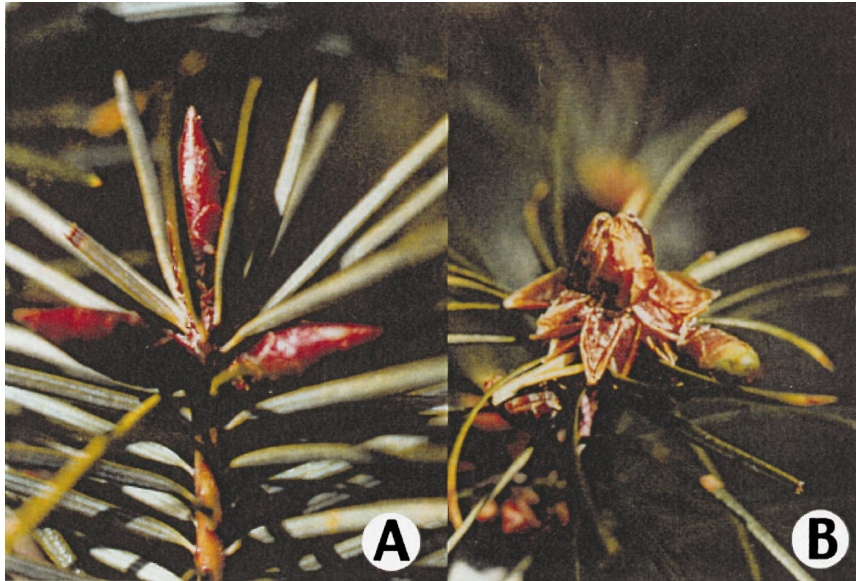


Fig. 1. (A) Normal Douglas-fir buds at ambient temperature and, (B) abnormal, rosetted Douglas-fir bud at elevated temperature.

production for the aerial portions of trees, alterations in bud morphogenesis may alter the branching patterns and allometry of trees (Niklas, 1994).

We hypothesize that at elevated temperature, the internal temperature of abnormal buds will be greater than that of normal buds. If present, an increase in internal bud temperature may initiate abnormalities in bud development by altering the developmental course of the temperature-sensitive shoot apex (MacDonald and Owens, 1993).

In this study of the effects of increased atmospheric temperature on Douglas-fir bud temperature, we used thermocouple probes to measure the internal temperature of buds of saplings grown in ambient and elevated (ambient + 4°C) temperature chambers (Tingey et al., 1996), and of normal and abnormal buds within the same elevated temperature chamber.

2. Materials and methods

2.1. Experimental design

Internal temperatures of *Pseudotsuga menziesii* (Mirb.) Franco, (Douglas-fir) buds were measured

in three ambient (AT) and three elevated temperature (+4°C above ambient), (ET) sun-lit controlled-environment chambers (Tingey et al., 1996) with 14 saplings per chamber. Saplings were exposed to temperature treatments from planting in summer, 1993, as bare-root, 2-year-old 'woods run' stock (Weyerhaeuser) until harvest in summer, 1997. Chamber dewpoints were adjusted in spring, 1994 to maintain the same vapor pressure deficit at ambient and elevated temperature. Trees were watered with deionized H₂O to maintain seasonal soil moisture variations typical of the southern Willamette Valley forests.

2.2. Bud temperature measurements

Internal bud temperatures were measured with 30 gage mini-hypodermic thermocouple probes, which were chosen to minimize bud disruption, (Type T, Copper-Constantan, Model HYP-1, Omega Engineering). Bud tips were pierced with 26 gage hypodermic needles prior to probe insertion. Type 2T subminiature connectors linked the probes to 20 AWG stranded copper constantan thermocouple extension wire connected to a multiplexer and a Campbell CR-10 Datalogger in an enclosure box. After probe calibration, measure-

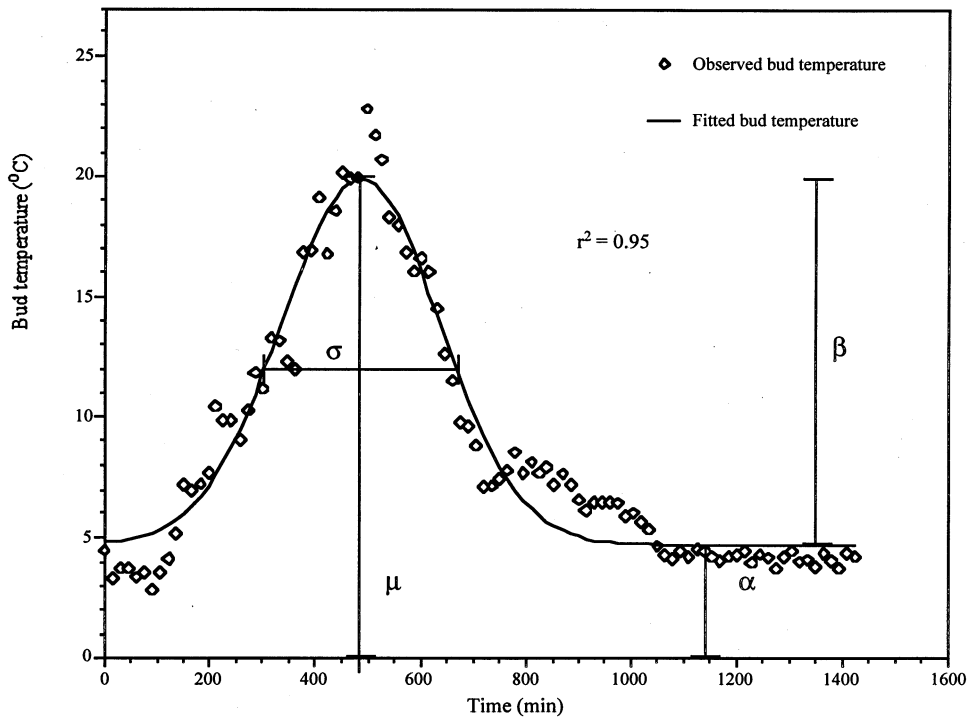


Fig. 2. Observed temperature of a single bud at ambient temperature fitted with nonlinear regression to a Gaussian curve of temperature over the course of a day with the following four parameters: α , minimum daily temperature; β , daily temperature range; μ , time of daily temperature maximum; and σ , time spread of the daily heating and cooling cycle. Observed temperatures were measured over a 5 day period from October 31, 1996 to November 4, 1996. Time measurements were adjusted for seasonal variation by defining time 0 as sunrise.

ments were acquired every 60 s and averaged every 15 min over the course of each experiment. Measurements were made on unshaded terminal branch buds or on adjacent lateral buds at mid-tree height but with different aspects to obtain buds at similar positions. Each bud was dissected and examined for the presence of internal abnormalities.

Internal temperatures of buds at ambient and elevated temperatures were compared by measuring five normal buds in an AT chamber concurrently with five buds in an ET chamber for each of the three pairs of AT/ET chambers. One pair of AT/ET chambers was monitored over the duration of each set of measurement dates (October 15–19, 24–28, and October 31–November 4, 1996).

Internal temperatures of normal and rosetted abnormal buds (Fig. 1) were compared by mea-

suring the internal temperatures of five outwardly normal buds and five outwardly abnormal, rosetted buds within each elevated temperature chamber (ET) over 4 days during these six measurement periods: November 7–12, 14–21, and 21–25, 1996, and February 2–11, 14–18, and 21–25, 1997.

2.3. Statistical analyses

Average diurnal curves for each bud were determined by averaging data collected over each experimental period at each 15 min interval. The resultant curves were averaged to obtain an average diurnal curve for each experimental treatment. Following the methods of Rubin et al. (1996) Gaussian curve was fitted to each average diurnal curve of temperature versus time using nonlinear regression (SAS Institute, 1987). A

Gaussian model was chosen because it fit the data curves well, and because its four parameters correspond to separate identifiable features of the diurnal curves: α , minimum daily temperature, β , daily temperature range, μ , time of daily temperature maximum, and σ , duration of the daily heating and cooling cycle (Fig. 2), which depicts observed and fitted data for a single bud. Time was adjusted by setting time 0 equal to sunrise to correct for seasonal changes in photoperiod. Because the datalogger recorded 60 min (1 h) as the value 100, we converted time to equal intervals and scaled the time of day from 0 to 1440 with this equation: (time of day – remainder) \times 60/100 + remainder.

We used multivariate analysis of variance (MANOVA) to test for mean differences in the four parameters (α , β , μ , and σ), of the diurnal temperature curves, with replication of experiments treated as a blocking factor. The

MANOVA tables for these analyses are shown in Table 1.

3. Results

3.1. Buds at ambient and elevated temperature

At elevated temperature, α was significantly higher ($P = 0.0001$), indicating a 2.4°C increase in daily temperature over ambient buds. At elevated temperature, bud temperature was 3.8°C higher during the late afternoon temperature peak, with a β of ($P = 0.0032$). No significant differences were found in μ ($P = 0.7407$), or σ ($P = 0.7407$), indicating no difference in the time of temperature maxima or the duration of the daily warming and cooling cycle.

3.2. Normal and abnormal buds at elevated temperature

Internal temperatures differed between normal and abnormal buds in each elevated temperature chamber (Fig. 3). Abnormal buds had a significantly higher β ($P = 0.0002$), indicating a higher daily temperature maxima and a greater temperature range. The offset of μ ($P = 0.0004$) in abnormal buds is evidence that their maximum temperature occurred earlier in the day. Normal buds had a higher σ ($P = 0.0024$), indicating a longer duration of the daily heating and cooling cycle. There was no significant difference in α ($P = 0.6956$), therefore, daily temperature minima were similar in normal and abnormal buds. All abnormal buds had internal abnormalities (Apple et al., 1998).

4. Discussion

The internal bud temperature increase that accompanied exposure to elevated temperature may contribute to alterations in morphogenesis of Douglas-fir buds (Apple et al., 1998). Shoot apices of Douglas-fir are sensitive to elevated temperature (MacDonald and Owens, 1993), and in rosetted buds they may not be well insulated

Table 1
MANOVA tables for analysis of bud temperature curve parameters in two types of experiments: (a) temperature treatment (ambient or elevated) effects on normal buds; and (b) bud type (normal or abnormal) effects under elevated temperature conditions (ambient +4°C)^a

Source	df
(a) Ambient or elevated temperature	
Temperature	1
Experiment (block)	2
Error	25
Total	28 (= 5 buds/temp. *2 temp. *three experiments, -1 missing value -1)
(b) Normal or abnormal buds	
Bud type	1
Experiment (block)	5
Error	48
Total	54 (= 5 buds/type *2 types *six experiments, -5 missing values -1)

^a In both cases, experiments were repeated at several times. Replication of experiments was treated as a blocking factor in the MANOVA.

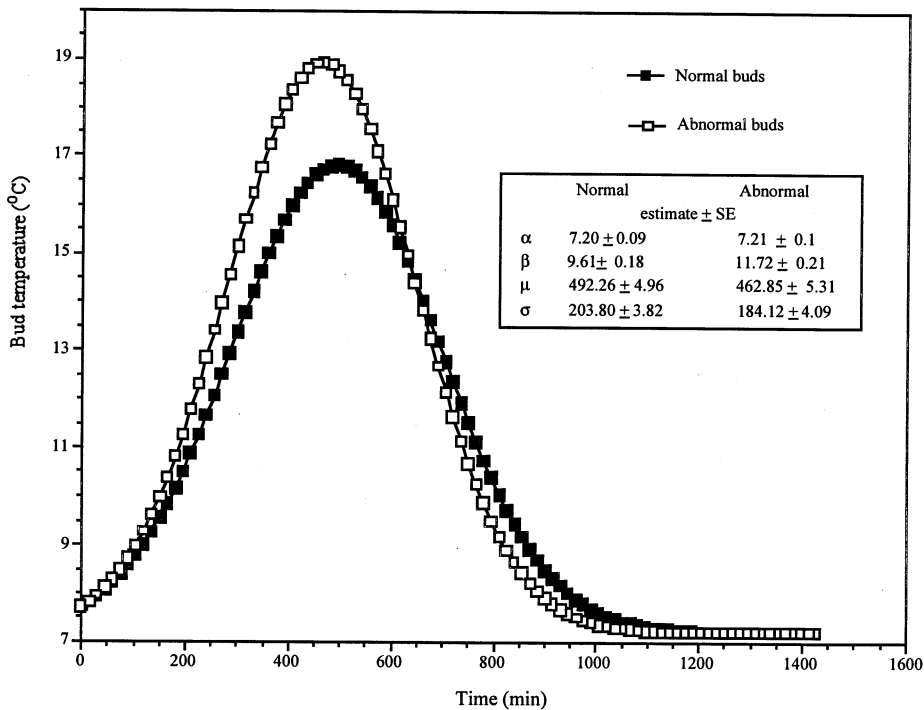


Fig. 3. Average Gaussian curves for diurnal temperatures of normal and abnormal buds grown at elevated temperature ($+^{\circ}\text{C}$) across six experiments (November 7–12, 14–21, 21–25, 1996, February 2–11, 14–18, 21–25, 1997; $n = 10$ for each date) with time measurements adjusted for seasonal variation by defining time 0 as sunrise.

(Smith, 1974; Rada et al., 1985). Rosetted buds may be subject to temperature fluctuations which may influence development. Buds on branch extremities may have a greater tendency towards temperature-induced developmental change, as they may be exposed to greater fluctuations in temperature, greater radiative heating, and may receive little shielding from incoming radiation.

The size, shape, and orientation of a plant organ can influence metabolic processes (Niklas, 1994). The reflexed outer scales of a rosetted bud form a ring that is somewhat perpendicular to the main bud axis and may contribute to the higher temperatures of rosetted buds by absorbing solar energy in a manner similar to that of a parabolic solar collector.

Sensitivity of bud development to elevations in temperature that are associated with potential climatic change may influence the growth and allometry of Douglas-fir trees in Pacific north-western forests.

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