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Effects of Low Temperature in Reactivated Cambial Cells Induced by Localized Heating During Winter Dormancy in Conifers

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ABSTRACT

Effects of low temperature on cambial cells induced by localized heating in *Cryptomeria japonica* and *Abies firma* were investigated during winter dormancy in January-February. Localized heating induced cambial reactivation in the stems earlier than natural cambial reactivation. In heated *Cryptomeria japonica* and *Abies firma* stems, cambial reactivation occurred after 6 and 2 days of heating, on 14 January 2007 and 15 January 2010, respectively. We stopped the electric heating system just after cambial reactivation in stems. When we stopped the heating system, the minimum atmospheric temperature was about 0°C. After cambial reactivation, due to rapid decrease in temperature, cell contents of cambium became coagulated but nucleus was present in ray cambial cells. After one month, the shrunk cambium produced new deformed tracheids with abnormal cell shape. The results suggest that rapid decrease in temperature just after cambial reactivation might induce temporary damage of cambium that produces deformed tracheids indicating that cambium and its derivatives can response directly to changes in temperature which provides a useful experimental model system for studies of cambial biology and xylogenesis.

Key words: Cambial activity, conifers, deformed tracheids, shrinkage of cambium, rapid decrease in temperature

INTRODUCTION

Wood is the product of the vascular cambium and wood formation depends on the cambial activity of trees (Catesson, 1994; Larson, 1994; Funada, 2008). In temperate zones, the vascular cambium of tree stems undergoes seasonal cycles of activity and dormancy, a phenomenon known as annual periodicity. This periodicity plays a critical role in the formation of wood. In late winter and early spring, new cell plates are formed in the cambium. The formation of new cell plates in spring is referred to as cambial reactivation (Catesson, 1994; Larson, 1994). Both the quantity and the quality of wood reflect the timing of cambial reactivation in temperate zones. Therefore, it is very important to develop a full understanding of the mechanism of wood formation and in particular, of cambial reactivation.

Winter dormancy is an important adaptive mechanism for the survival of perennial plants and trees in temperate and cold climates. The timing of phases of cambial activity and dormancy is controlled by both environmental and genetic factors. In trees, dormancy is established in advance

of the cold season and the termination of winter dormancy is a physiological process that requires timely environmental and internal signals.

The cambial activity of coniferous trees in temperate zones is characterized by the formation of earlywood and latewood (Larson, 1964; Denne and Dodd, 1981; Timell, 1986; Schweingruber, 1988). The onset of cambial activity is strongly influenced by the environment (Schweingruber, 1988) and it has been proposed that the maximum growth rate of trees might be regulated by temperature (Rossi *et al*., 2007). Studies of the physiology and dendrochronology of cambial activity indicate that temperature is closely associated with the radial growth of tree stems (Denne and Dodd, 1981; Schweingruber, 1988; Fonti *et al*., 2007; Rossi *et al*., 2007; Schmitt *et al*., 2004). In addition, Makinen *et al*. (2003) suggested that the annual maximum growth rate of the cambium in *Picea abies* might be regulated by temperature. By contrast, Rossi *et al*. (2006) reported that, in conifers such as *Abies*, *Larix*, *Picea* and *Pinus,* the maximum growth rate occurs at approximately the same time as maximum day length. However, the physiological regulation of cambial activity in the spring is still not fully understood (Funada *et al*., 2002).

Evidence for the earlier induction of cambial reactivation by localized heating suggests that increases in the temperature of the stem might be the limiting factor in the onset of cambial reactivation during the quiescent stage of dormancy (Barnett and Miller, 1994; Begum *et al*., 2007b, 2008, 2010a, b, 2012; Gricar *et al*., 2006; Oribe and Kubo, 1997; Oribe *et al*., 2001, 2003). In addition, the patterns of cambial reactivation and xylem differentiation were almost identical to those in natural systems. Therefore, we postulated that artificial heating might provide a good model system to investigate the cambial biology of trees. Such a model system would allow us to compare detailed cambial activity and xylem differentiation directly over relatively short periods of time (Oribe and Kubo, 1997; Oribe *et al*., 2001; Begum *et al*., 2007b, 2010a, b). Present observations showed that an artificial increase in temperature can induce cambial reactivation in a hardwood and conifers. However, the effects of rapid decrease in temperature after cambial reactivation and xylem differentiation remain to be clarified.

The main purpose of the present study was to investigate whether decrease in temperature after cambial reactivation can induce any changes in cambial cells and xylem differentiation continue or not in *Cryptomeria japonica* and *Abies firma* trees. Therefore, this paper analyzed the effects of rapid decrease in temperature on the cambium by using heated cambial reactivation system in adult trees of *Cryptomeria japonica* and in *Abies firma* seedlings that can be used as a good system for studies of xylogenesis. Cambial reactivation that induced by localized heating was stopped just after cambial reactivation to observe the effects of rapid decrease in temperature on cambial cells. In addition, presence of nucleus in heated-reactivated cambial cells and non-heated cambial cells were examined to clarify the status of cambial cells whether the cells were alive or not. The possible mechanism of cambial activity in relation with decrease in temperature will be discussed.

MATERIALS AND METHODS

Plant materials: Two adult *Cryptomeria japonica* trees which were 71 and 93-years-old and 56 *Abies firma* seedlings of 3-years-old were growing in the field nursery of the Tokyo University of Agriculture and Technology in Fuchu, Tokyo (35°40' N, 139°29' E; 40 m above the sea level), Japan, were used in this study. The *Cryptomeria japonica* trees were examined from 8 January 2007 to 28 February 2007 and *Abies firma* seedlings were examined from 13 January 2010 to 3 March 2010.

Heat treatment: In case of adult *Cryptomeria japonica* trees, electric heating tape (Silicone-Rubber Heater; O and M Heater, Nagoya, Japan), 50 cm in length and 30 cm in width, was wrapped at one side of the main stem of each tree at breast height (Fig. 1a) (Oribe and Kubo, 1997; Oribe *et al*., 2001, 2003; Begum *et al*., 2007b, 2010a, b). In case of *Abies firma* seedlings, electric heating ribbon (Nippon Heater Co., Ltd. Tokyo, Japan), 6 m in length and 0.5 cm in width, was encircled at the entire stem base of each seedling one by one (Fig. 1b). The temperature between the outer bark and the heating tape was recorded with a thermometer and, at the site at which the stem was heated; the temperature was adjusted to 20-22°C with a thermostat. No abnormal structures were found by naked eyes in the stems after artificial heating.

In adult *Cryptomeria japonica* trees and *Abies firma* seedlings, localized heat treatment was started from 8 January 2007 and 13 January 2010, respectively. Continuous heating was applied until cambial reactivation and heating system was stopped on 18 January 2007 and 19 January 2010 in both species, respectively. After stop of heating, samples were collected from heated and non-heated control portions of the stem until 27 February 2007 and 3 March 2010, in both cases, respectively.

Collection of samples: In case of adult *Cryptomeria japonica* trees, samples were taken at three to four days intervals from heated stems and non-heated stems under natural conditions throughout the sampling period. A series of small blocks (2×2×1 cm^3) which contained phloem, cambium and some xylem cells, was removed with a disposable scalpel and chisel with a zigzag fashion to eliminate any effects of wounding from heated stems and stems under natural conditions. Each block was cut into 2 mm thick samples immediately after removal from the tree.

In case of *Abies firma*, four sample seedlings (two from heated stem and two from non-heated control stem) were cut in every sampling date at one day interval until 19 January 2010. Then sampling was done at one week interval until 3 March 2010. For non-heated control sample, we used seedling that was not heated and sample was taken from the same portion of stem at 2-3 cm above the stem base. In each sampling date, we tried to collect the seedlings that had almost the same stem height and diameter to avoid any differences among seedlings. The heated and non-heated control portion of stems was cut into 2 mm thick samples immediately after removal from the tree.

Fig. 1(a-b): (a) Electric heating tape was wrapped at one side of the main stem of adult *Cryptomeria japonica* trees and (b) electric heating ribbon was encircled at the entire stem base of the seedling of *Abies firma* one by one

Preparation of samples for light microscopy: The samples were fixed in 4% glutaraldehyde in 0.1 M phosphate buffer (pH 7.3), under a vacuum, for 1 h at room temperature. Fixed samples were washed in 0.1 M phosphate buffer and trimmed to 3 mm in length for subsequent fixation in 1% osmium tetroxide in 0.1 M phosphate buffer for 2 h at room temperature. After washing in phosphate buffer, specimens were dehydrated in a graded ethanol series and embedded in epoxy resin. Transverse sections were cut at a thickness of approximately 1 and 40 μm with a glass knife on an ultramicrotome (Ultracut N; Reichert, Vienna, Austria) and freezing stage of a sliding microtome for sequential observations of cambial reactivation and presence of nuclei. Sections were stained with a solution of 1% safranine in water or 1% aqueous solution of acetocarmine for observations of cambial reactivation and presence of nuclei in cambial cells and then examined under a light microscope (Axioscop; Carl Zeiss, Oberkochen) (Murakami *et al*., 1999; Nakaba *et al*., 2006; Begum *et al*., 2007b, 2008, 2010a, b).

Air temperatures during experiments: Daily maximum, average and minimum air temperatures during each experimental period were obtained from the Japan Meteorological Agency that located in Fuchu, Tokyo. Maximum, average and minimum air temperatures from 1 January to 31 March 2007 (during the first experiment for *Cryptomeria japonica*) and from 1 January to 31 March 2010 (during the second experiment for *Abies firma*) are shown in Fig. 2. After stop of heating, in February 2007, the minimum temperature was -2.4 to 8.4°C, the maximum temperature was 6.6 to 17.5°C and the average temperature was 2.9 to 10.2°C (Fig. 2a). In

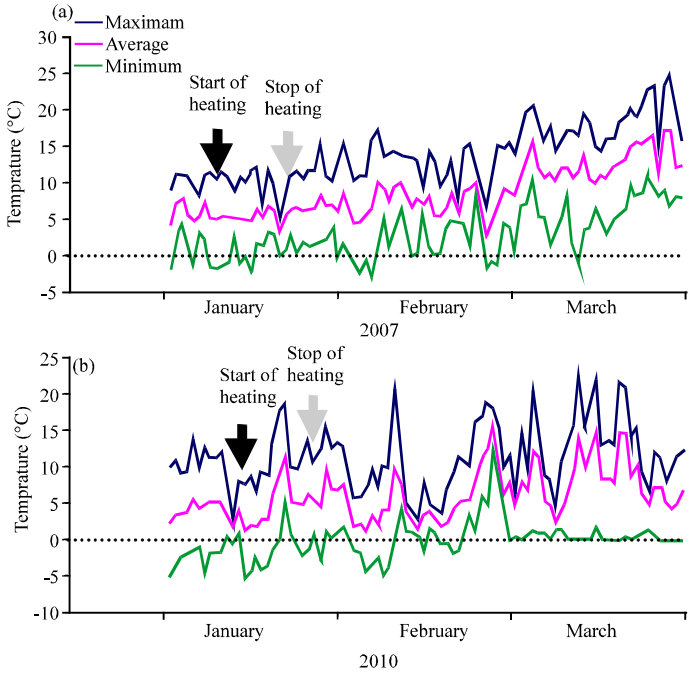

Fig. 2(a-b): Records of the maximum, average and minimum daily air temperatures at the experimental site in Fuchu, Tokyo, (a) from 1 January 2007 to 31 March 2007 and (b) from 1 January 2010 to 31 March 2010 (b). Black arrows indicated the time of start of heating, grey arrows indicated the time of stop of heating and horizontal dotted lines indicated the level of 0°C in 2007 and 2010

February 2010, the minimum temperature was -4.9 to 12.3°C, the maximum temperature was 2.8 to 20.9°C and the average temperature was 1.9 to 11.4°C (Fig. 2b).

RESULTS

Dormant cambium: No division of fusiform cambial cells and ray cambial cells was detected in samples of cambium of *Cryptomeria japonica* and *Abies firma* that had been collected on 8 January 2007 and 13 January 2010, respectively (Fig. 3a, b) indicating that the cambium was dormant. The cambium was located between the previous year's sieve cells and the narrow-diameter thick-walled latewood tracheids that had formed during the previous growing season (Fig. 3a, b). During dormancy, the cambium consisted of five or six radial layers of radially narrow and compactly arranged cells (Fig. 3a, b).

Timing of cambial reactivation and xylem differentiation in heated stems: In heated *Cryptomeria japonica* and *Abies firma* stems, cambial reactivation occurred after 6 days and 2 days of heating, on 14 January 2007 and 15 January 2010, respectively (Fig. 3c, d). After production

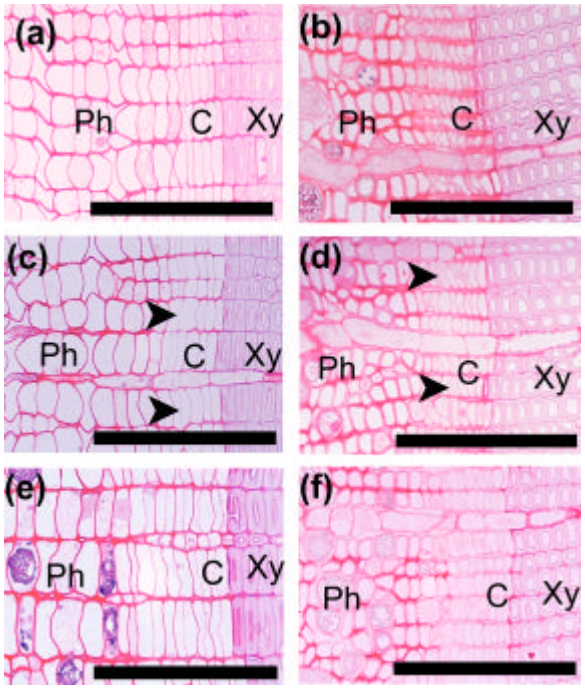

Fig. 3(a-f): Light micrographs showing that transverse views of cambium collected from heated stems of *Cryptomeria japonica* and *Abies firma*. Cambial cells were arranged very compactly and the cambial zone consisted of four or five layers of fusiform cambial cells (a) on 8 January 2007 in *Cryptomeria japonica* and (b) on 13 January 2010 in *Abies firma* stems, respectively. New cell plates (arrowheads) were evident in cambial cells on (c) 14 January 2007 and (d) on 15 January 2010 in both species, respectively. Heating system was stopped on 18 January 2007 and on 19 January 2010 when 6-7 radial files of cambial cells were produced (e) in *Cryptomeria japonica* and (f) in *Abies firma* stems, respectively. C: Cambium; Ph: Phloem; Xy: Xylem. Bars = 100 μm

of 5-6 radial files of fusiform cambium on 18 January 2007 in *Cryptomeria japonica* and on 19 January 2010 in *Abies firma*, heating system was stopped in both species (Fig. 3e, f).

Effects of rapid decrease in temperature on cambial cells after stop of heating: One week later of stop of heating, on 25 January 2007 and 26 January 2010, the cambial cells became shrunk and cell contents coagulated in phloem and cambial cells in adult *Cryptomeria japonica* trees and *Abies firma* seedlings (Fig. 4a, b). The higher magnified image of the same portion of Fig. 4a showed that, in the cambial cells, cell contents became coagulated (Fig. 4c). At that time the structure, shape and size of cambial cells were not at normal condition (Fig. 4a-c). Two weeks later of stop of heating, on 1 February 2007 and 2 February 2010, the cambial cells were almost at the same condition as well as shrunk cambium observed in both species (Fig. 4d). In addition, no new cell plates were observed in the cambial zone of *Cryptomeria japonica* and *Abies firma* stems indicating that cambial activity was reduced or almost stopped (Fig. 4a-d). Two weeks later of stop

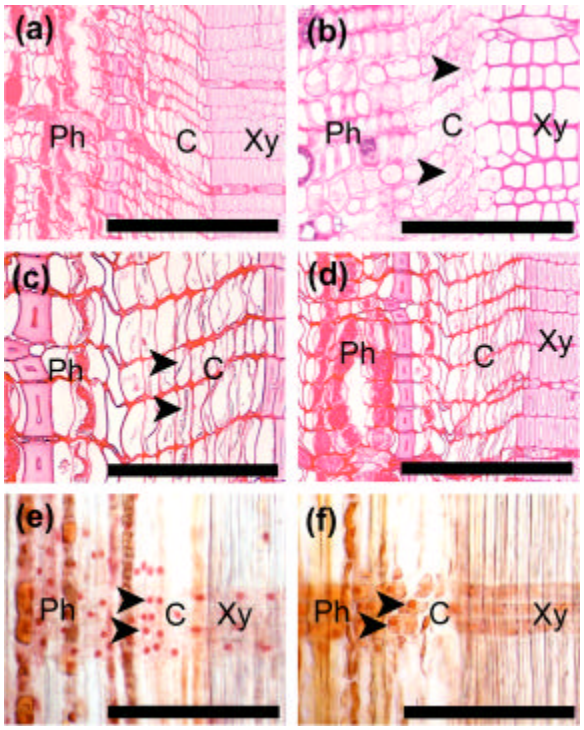

Fig. 4(a-f): Light micrographs showing that transverse views of cambium collected from heated stems of *Cryptomeria japonica* and *Abies firma*. After one week of stop of heating, coagulated cell contents (arrowheads) were observed (a) in *Cryptomeria japonica* and (b) in *Abies firma* stems. Higher magnification of Fig. 4a showed that longitudinal phloem parenchyma cells and (c) cambial cells became shrunk. After two weeks of stop of heating, still coagulated cell contents were observed (d) in *Cryptomeria japonica* stems. Arrowhead showing nucleus (e) in shrunk cambium after one week of stop of heating and nucleus (f) in non-heated cambial cells. C: Cambium; Ph: Phloem; Xy: Xylem. Bars = 100 μm

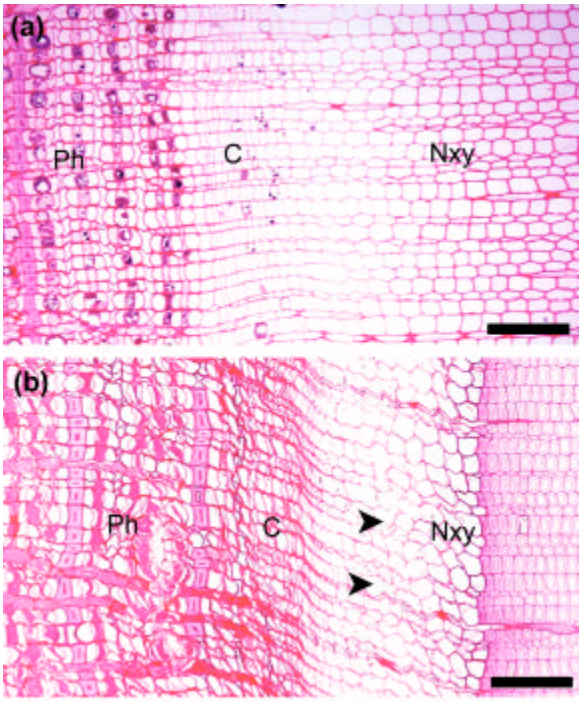

Fig. 5(a-b): Light micrographs showing that transverse views of cambium collected from heated stems of *Cryptomeria japonica*. (a) Xylem differentiation occurred in non-heated control stems and (b) formation of new deformed xylem cells (arrowheads) from shrunk cambium in heated stems after one month of stop of heating in *Cryptomeria japonica*. C: Cambium; Ph: Phloem; Nxy: New xylem. Bars = 100 μm

of heating, on 1 February 2007 and 2 February 2010, in the same sample of *Cryptomeria japonica* and *Abies firma*, nucleus was present in ray cambial cells (Fig. 4f) indicating that the cells were still alive as normal cambial cells (Fig. 4e). After one month of stop of heating, on 18 February 2007, the shrunk cambium produced new tracheids with deformed structure of secondary xylem as compared with the normal xylem differentiation in *Cryptomeria japonica* trees (Fig. 5a, b).

Relationship between shrinkage of cambium and temperature data: During localized heating, we applied a constant temperature of 20-22°C both in *Cryptomeria japonica* and *Abies firma* stems. Due to the stop of heating, temperature decreased rapidly in the heated portions of the stems in both species (Fig. 2). When we stopped the heating system in February, the minimum atmospheric temperature was ranged from -2.4 to 0°C and from -4.9 to 1.2°C in 2007 and 2010, (Fig. 2), respectively. Therefore, cambium of those species received a temperature from 22°C to around 0°C after cambial reactivation. The temperature profile and microscopic images of cambial cells clearly showed that shrunk cambium with coagulated cell contents produced due to rapid decrease in temperature in adult *Cryptomeria japonica* trees and *Abies firma* seedlings in February (Fig. 2, 4a-d, 5b).

DISCUSSION

Rapid decrease in temperature on localized-heated stems induced coagulation of cell contents in cambial cells with deformed shape and size of phloem cells in *Cryptomeria japonica* trees and *Abies firma* during winter dormancy in February. One week later of stop of heating, shrunk with abnormal structure of longitudinal phloem parenchyma cells were observed in localized-heat-induced differentiating phloem cells. In our previous research, we observed that due to the rapid decrease in temperature, cell wall thickening of phloem fibers started earlier than xylem cells in *Cryptomeria japonica* trees and *Abies firma* stems. In addition, division of phloem cells started prior to cambial reactivation and xylem differentiation in heated stems and under natural conditions at warmer early spring of hybrid poplar (*Populus sieboldii* × *Populus grandidentata*), indicating that phloem cells were able to make quick response to increase in temperature than cambial cells and xylem cells (Begum *et al*., 2007b, 2008). In present study, it was found that coagulation of cell contents occurred in longitudinal phloem parenchyma cells due to stop of heating. This observation suggests that phloem cells might respond to decrease in temperature more rapidly than xylem cells in conifers.

It was already proved that temperature was a limiting factor in the onset of cambial reactivation and xylem differentiation during the quiescent dormant state in conifers (Savidge and Wareing, 1981; Barnett and Miller, 1994; Oribe and Kubo, 1997; Oribe *et al*., 2001, 2003; Gricar *et al*., 2006; Begum *et al*., 2010a, b) and in a hardwood hybrid poplar (Begum *et al*., 2007b). Increase in temperature or warmer early spring induced earlier cambial reactivation and xylem differentiation in trees (Oribe and Kubo, 1997; Oribe *et al*., 2001, 2003; Gricar *et al*, 2006; Begum *et al*., 2007b, 2008, 2010a, b). Similarly, in the present study, earlier cambial reactivation and xylem differentiation was induced by localized heating in *Cryptomeria japonica* trees and *Abies firma* stems during winter dormancy in February indicating that temperature is one of the most important trigger for start of cambial reactivation.

Cambial reactivation occurred when the minimum temperature exceeded 0°C for 9 to 12 days in hybrid poplar (*Populus sieboldii* × *Populus grandidentata*) and 8-10 days for *Cryptomeria japonica* trees (Begum *et al*., 2008, 2010a). In addition, we previously observed that, the maximum daily temperature often exceeded 10°C but the minimum temperature was sometimes below 0°C. Under these conditions, no formation of new cell plates occurred in the cambium in March in *Cryptomeria japonica* trees (Begum *et al*., 2010a). Thus, low temperatures appear to be very important for maintenance of a quiescent state (Begum *et al*., 2008, 2010a). Therefore, previously we hypothesized that minimum temperature above 0°C might be critical for cambial reactivation in the stems of deciduous hardwood hybrid poplar (*Populus sieboldii* × *Populus grandidentata*) and *Cryptomeria japonica* trees (Begum *et al*., 2008, 2010a). In our present study, it was observed that rapid decrease in temperature in heated reactivated cambium induced shrinkage of cambial cells with coagulation of cell contents. In addition, nucleus was observed in those shrunk cambial cells indicating that cambial cells were alive. Therefore, it appears that rapid changes in environmental conditions might induce cellular changes in cambial cells.

Certain abnormal environmental conditions can induce the formation of various structures, For example, wider tracheids were produce under water stress condition in plants (Landrum, 2008; Gutierrez *et al*., 2009). Salinity stress decreased xylem exudation rate and collapsed xylem cells (Kabir *et al*., 2004). Drought stress increased vessel wall thickness (Mostajeran and Rahimi-Eichi, 2008) and showed highest cell wall associated peroxidase activity in leaf cells (Hamad *et al*., 2004). Low temperature induced greater degree of shrinkage in cell structure (Singh and Pandey, 2011).

Chilling strees decreased stomatal conductance and increased peroxidase enzymatic activity in plant cells (Islam *et al*., 2011) and methyl jasmonate suppressed chilling injury and water loss. In general, with increasing methyl jasmonate concentration, chilling injury reduced significantly (Zolfagharinasab and Hadian, 2007). Deflowering of rachis induced narrower xylem cells which inhibit water conduction to the top of the rachis resulted few or smaller sized pod production (Begum *et al*., 2007a). Thus, environmental stress plays a significant role on morphology and structure of cells in plant.

In our previous research, we observed that cambial reactivation and xylem differentiation occurred above a certain maximum threshold value such as for hybrid poplar (*Populus sieboldii* × *Populus grandidentata*) the threshold temperature was 15°C and for *Cryptomeria japonica* it was 10 or 11°C (Begum *et al*., 2008, 2010a). It was also reported that continuation of cambial activity and xylem differentiation required a constant threshold maximum temperature (Begum *et al*., 2008, 2010a). In our present study, the subsequent rapid decrease in temperature from 22 to around 0°C during active cambial cell division in localized-heat-induced stem resulted stopping of cambial activity with shrinkage of cambial cells in *Cryptomeria japonica* and *Abies firma* stems. The results suggest that cambial activity was stopped due to rapid changes of temperature in February.

The present results showed that localized heating during cambial dormancy induced earlier cambial reactivation in conifers and subsequent rapid decrease in temperature just after cambial reactivation induced formation of shrinkage cambium. The results suggest that low temperature might changes endogenous balances that induced shrinkage of cambium with deformed structure of differentiating tracheids which would be helpful to study the mechanism of cambial activity in conifers. In addition, in the present research we observed that without any obvious changes of day length, supply of photosynthates and auxin, only rapid decrease in temperature might have a direct effect on reduction or stopping of cambial activity in *Cryptomeria japonica* and *Abies firma* trees.

It can be concluded that rapid decrease in temperature might be expected to have a direct effect on continuous cambial cell division in *Cryptomeria japonica* and *Abies firma* stems. Due to stop of heating, cambium and its derivatives received a rapid decrease in temperature from around 22 to 0°C that induced coagulation of cell contents in cambial cells and phloem cells of *Cryptomeria japonica* and *Abies firma* stems. The results indicate that cambium and its derivatives can response directly to changes in temperature. Finally, it can be concluded that rapid decrease in temperature might be one of the most important factor that regulate continuous normal cambial cell division in conifers indicating that earlier cambial reactivation might have risk of frost damage because cold tolerance decreases after cambial reactivation.

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