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ORIGINAL ARTICLE

Physiological and Biochemical Traits of Dormancy Release and Growth Resumption in Japanese Cedar in the Warm-Temperate Zone

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Abstract

Global warming will disturb dormancy release and growth resumption of trees. To better understand this process, it is important to investigate physiological and biochemical traits related to these stages. We examined dormancy release and growth resumption in Japanese cedar (*Cryptomeria japonica* [L.] D. Don), an evergreen needle-leaved tree, in the warm-temperate zone by evaluating budbreak under growth-promoting conditions, and simultaneously examining respiration rates and contents of carbohydrates and phytohormones in shoots from November 2022 to March 2023. A long time to budbreak and the lowest budbreak rates of 75% in November indicated shallow dormancy. Budbreak rates of 98%, short time to budbreak, and first appearance of budbreak in the field in March indicated growth resumption. Continuous changes in budbreak rates and time to budbreak between dormancy and growth resumption indicated dormancy was gradually released. Surges in budbreak rates in December indicated dormancy was almost completely released by early winter. Contents of abscisic acid (ABA) and salicylic acid (SA) decreased from November, remained low in March, and were strongly associated with budbreak rates according to principal component analysis. It was suggested that the depletion of SA led to the depletion of ABA, contributing to dormancy release and growth resumption. Fructose and *trans*-zeatin accumulated until February, and low levels of starch, indole-3-acetic acid, jasmonic acid, and jasmonic acid-isoleucine during winter was followed by accumulation in March. Although these biochemical traits were less related to budbreak rates compared to ABA and SA, they seemed to assist either dormancy release or growth resumption.

Study Implications

In response to the threat of global warming to forests, there is a pressing need to understand the mechanism of dormancy release in trees. In this study, we observed physiological and biochemical traits related to dormancy release in the Japanese

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cedar (*Cryptomeria japonica* [L.] D. Don). We found that abscisic acid and salicylic acid were specifically related to the process of dormancy release, while other phytohormones, carbohydrates, and respiration were less related to dormancy release. Moreover, the possible interrelationships between physiological and biochemical traits hypothesized in this study will help future research to unravel the mechanism of dormancy release.

Keywords Japanese cedar · Warm-temperate zone · Dormancy release · Growth resumption · Physio-biochemical traits

Introduction

Trees growing in the temperate zone show clear seasonality, actively photosynthesizing and investing in growth in summer, preparing to cease growth in autumn, and stopping growth by the time winter arrives. This growth cessation stage in winter is called dormancy, and is characterized by the inability to grow (i.e., budbreak) even under growth-promoting conditions (Rohde and Bhalerao 2007). Depending on the level of growth suppression, dormancy can be divided into two types, i.e., deep dormancy and shallow dormancy (Nagata and Sasaki 2002; Jewaria et al. 2021). Deep dormancy is typically seen in species growing in high latitudes such as broadleaf deciduous trees. Deep dormancy is characterized by a strong budbreak suppression period; for instance, grapevine (*Vitis vinifera* L.) shows a period of budbreak rates less than 5% (Ben Mohamed et al. 2010), and Japanese pear (*Pyrus pyrifolia* [Burm. f.] Nakai; Ito et al. 2012) and Chinese plum (*Prunus mume* [Siebold] Siebold & Zucc.; Zhang et al. 2018) shows a period of budbreak rates of 0% under growth-promoting conditions. On the other hand, shallow dormancy is seen in species growing in low latitudes such as broadleaf evergreen species. In these species, even at the period with the strongest budbreak suppression effect, budbreak rates are higher than 50% (Yurugi and Nagata 1981; Nagata and Yurugi 1990; Zhang et al. 2021a, b).

In both types of dormancy, a certain period of low air temperature exposure (i.e., chilling) is required to release dormancy (Du et al. 2019; Song et al. 2020; Wang et al. 2024a, b), and growth resumes in spring as indicated by budbreak. Global warming is expected to reduce the amount of chilling by shortening the period of low air temperature in winter (Baldocchi and Wong 2008; Luedeling et al. 2009), thereby disturbing the release of dormancy. A possible scenario could be the delayed timing of budbreak, a globally observed trend in recent years (Wang et al. 2022), which could prevent frost damage from cold spells during the growth resumption stage in spring (Mura et al. 2022). However, an alternative scenario could be the abortion or abnormal budbreak in spring (Yamane 2014; Fadón and Rodrigo 2018; Tominaga et al. 2022), which would result in impaired growth and/or reproduction of the tree. As these phenomena are thought to be caused by physiological and biochemical abnormality (Tominaga et al. 2022), the

key to predict these phenological events would be to understand the physiological and the biochemical mechanisms that regulate the release of dormancy and the resumption of growth.

Various studies, especially in species that show deep dormancy, have helped to pinpoint some of the physiological and biochemical traits involved in the mechanism of dormancy release and growth resumption (Beauvieux et al. 2018; Fadón and Rodrigo 2018). In many cases, physiological traits like respiration rates and biochemical traits such as contents of carbohydrates and phytohormones change markedly during dormancy release and/or growth resumption (e.g., Ito et al. 2012; Parada et al. 2016; Gao et al. 2021; Hiejima et al. 2024). Such changes suggest the mediatory roles of these traits in the growth regulation process, i.e., the budbreak regulation process (Arora et al. 2003; Lloret et al. 2018; Liu and Sherif 2019; Fadón et al. 2020), as well as the interrelationships of these traits (e.g., Parada et al. 2016; Liu and Sherif 2019; Sami et al. 2019). In order to better understand how each physiological or biochemical trait affects the other, simultaneous observation of the traits is necessary.

However, different studies have found diverging effects of physiological and biochemical traits over dormancy release and growth resumption. For example, starch contents are high during dormancy and become depleted toward the resumption of growth in shoots of Japanese pear (Ito et al. 2012) and in buds of Chinese plum (Zhang et al. 2018), but are low during dormancy and then increase toward the resumption of growth in shoots of English oak (*Quercus robur* L.; Morin et al. 2007) and buds of grapevine (Rubio et al. 2019). Differences in contents between species have also been observed for phytohormones: the contents of abscisic acid begin to decrease during dormancy in shoots of fig (*Ficus carica* L.; Kawamata et al. 2002) and buds of Chinese plum (Zhang et al. 2018), whereas the contents remain high during dormancy and begin to decrease at the end of dormancy in buds of sweet cherry (*Prunus avium* L.; Chmielewski et al. 2017). Such findings suggest that the physiological and the biochemical mechanism underlying the process of dormancy release and growth resumption is not ubiquitous among species, and species-specific investigations of physiological and biochemical traits are required.

Japanese cedar (*Cryptomeria japonica* [L.] D. Don) is an evergreen needle-leaved coniferous species that is used for timber production in the temperate zone of East Asia, and its wood product is exported globally. Despite its importance in forestry, knowledge of its dormancy and release is still rudimentary. The process of dormancy release and growth resumption in Japanese cedar may be severely hindered in the warm-temperate zone as global warming progresses, since the period of low air temperature in this zone is shorter than at higher latitudes (Ayerza and Sibbett 2001). In addition, the dearth of studies on the process of dormancy release and its related physiological and biochemical traits of trees in conditions with reduced chilling (e.g., Beil et al. 2021; Götz and Chmielewski 2021; Garrigues et al. 2023; Hiejima et al. 2024) renders it difficult to predict how Japanese cedar will behave in an environment with scarce chilling.

The objective of this study was to investigate changes of physiological and biochemical traits related to dormancy release and growth resumption over time in Japanese cedar growing in the warm-temperate zone. We first hypothesized that Japanese cedar, as an evergreen tree, displays a form of shallow dormancy. Secondly,

we hypothesized that dormancy releases at the end of winter and resumes growth in spring due to the warm environment (i.e., warm-temperate zone). Finally, we hypothesized that by evaluating respiration rates, carbohydrate contents, and phytohormone contents, we could observe specific traits related to dormancy release, such as the gradual recovery of respiration, accumulation of sugars, and the depletion of growth-inhibiting phytohormones, as well as certain traits associated with growth resumption, including the accumulation of growth-promoting phytohormones and starch as an energy source for growth.

Materials and Methods

Study Site

The physiological and biochemical traits related to the release of dormancy and the resumption of growth were evaluated in 110 trees which were randomly selected from 3-year-old Japanese cedar (cv. Obiaka), an evergreen needle-leaved tree, growing on a plantation site (0.34 ha) in the Takakuma Experimental Forest, southern Kyushu, Japan (N31°31′122″, E130°46′676″, elevation 467 m) from November 21, 2022 to March 30, 2023. This site is in the warm-temperate zone, with temperatures in winter occasionally falling below freezing (Yonemura et al. 2021). The annual mean air temperatures at the study site in 2022 and 2023 were 15.0 °C and 15.6 °C, respectively (Takakuma Experimental Forest database 2023). During the winter of 2022–2023, western Japan including Kyushu did not experience air temperature anomalies: the normalized temperature anomalies were close to ± 0.0 °C (Japan Meteorological Agency 2023). However, in our study site, compared with the monthly mean air temperature over the period of November 2010 to March 2022 (Takakuma Experimental Forest database 2023; data only available from November 2010 onwards), the values during the experimental period were 1.6 °C, 1.0 °C, 2.6 °C, and 4.2 °C higher in November, January, February, and March, respectively (Fig. 1a); the value in December was 0.9 °C lower (air temperature in our experiment was recorded using a data logger; DL-171, AS ONE, Osaka, Japan). December and January were the coldest months in our experimental period with monthly mean air temperatures recording 5.5 °C and 5.6 °C, respectively. In addition, January had the lowest daily minimum air temperature, with a recorded value of − 8.4 °C (Fig. 1b). The total amounts of precipitation in 2022 and 2023 were 2027.0 and 3628.5 mm, respectively (Takakuma Experimental Forest database 2023). The total amount of precipitation during the experimental period was 693.5 mm, with January 14 recording an extremely high value of 111.5 mm (Fig. 1c).

Determination of Dormancy Release and Growth Resumption

We selected 20 different trees of the 110 trees on each sampling date, i.e., November 21, December 25, 2022, January 27, February 28, and March 30, 2023 (in total, 100 of the 110 trees were used). From each tree, we sampled

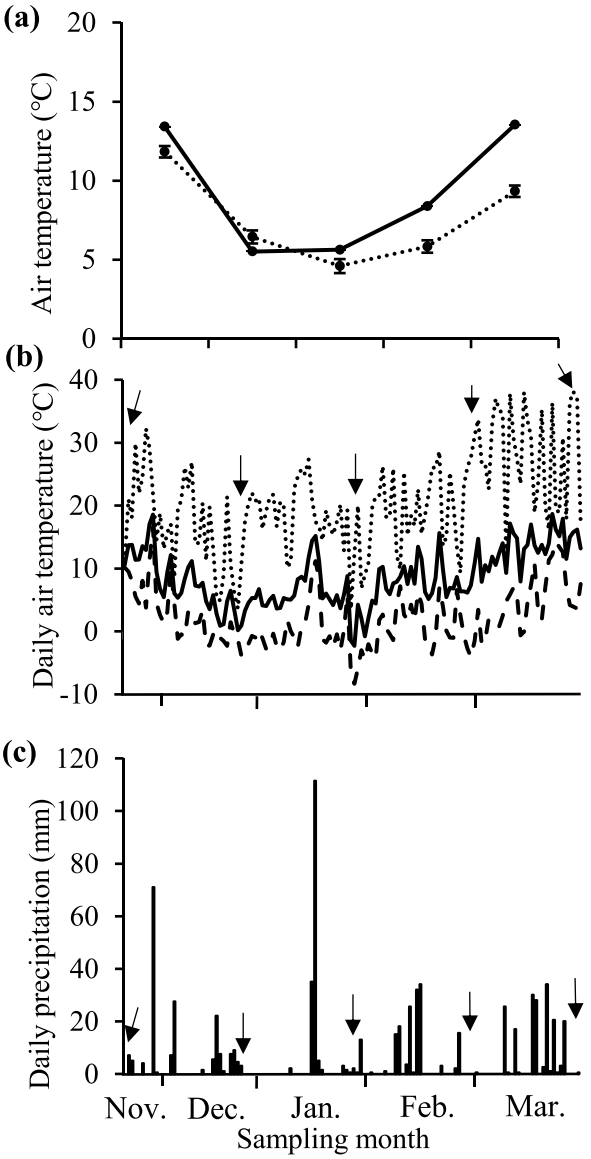


Fig. 1 **a** Air temperature at the study site during the experimental period (November 2022 to March 2023; solid line) and over the period of November 2010 to March 2022 (dotted line). **b** Daily air temperature at the study site during the experimental period. The solid line shows the daily mean air temperature, and the dashed line and dotted line show the daily minimum air temperature and daily maximum air temperature, respectively. Arrows indicate the starting point of sampling in each month. **c** Daily precipitation at the study site during the experimental period. Arrows indicate the starting point of sampling in each month

five shoot cuttings (100 shoot cuttings were used every month), and immediately immersed their bases in a container filled with water. After transferring the shoot cuttings to the laboratory, their lengths were adjusted to 15 cm with scissors, placed in test tubes filled with deionized water, checked for any new leaf formation (i.e., budbreak) at the main stem, and incubated for 30 days (Mochioka et al. 1996; Ben Mohamed et al. 2010; Parada et al. 2016) in a phytotron (CLH-301; Tomy Seiko Ltd., Tokyo, Japan) under growth-promoting

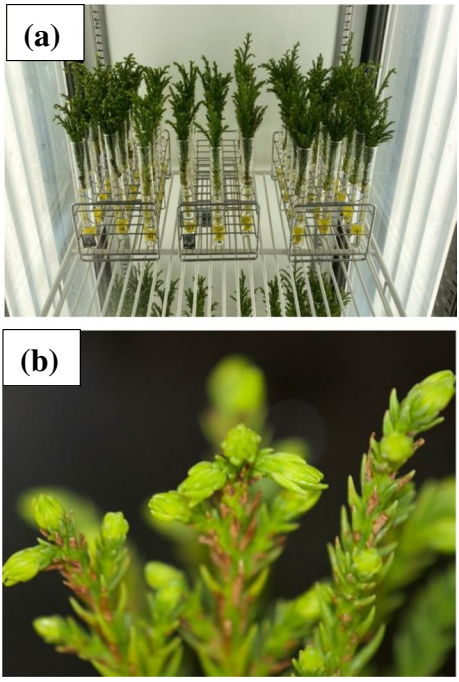


Fig. 2 **a** Shoot cuttings incubated in a phytotron at 25 °C (day)/22 °C (night) with a 16-h photoperiod illuminated with white fluorescent light at 228 µmol m^{-2} s^{-1}, and (**b**) shoot cuttings with budbreak after 30 days of incubation

conditions (Fig. 2) consisting of a 16-h photoperiod with an air temperature of 25 °C as described by Nose et al. (2020). The air temperature was also set to drop to 22 °C at night with a constant humidity of 75%. Every 5 days, deionized water in the test tubes was changed and a small part of the base of each shoot cutting was cut to prevent vessel occlusion by algal growth (Dennis 2003; Ben Mohamed et al. 2010). In addition to the first transfer to the phytotron (i.e., day 0 of incubation), we recorded budbreak at the main stem for each shoot cutting every five days starting from day 15 of incubation (i.e., day 15, 20, 25, and 30 of incubation). The budbreak rate after 30 days of incubation for each tree was calculated using Eq. 1: Budbreak rate of each tree (%) = No. of shoot cuttings with budbreak/No. of shoot cutting replicates × 100 [Eq. 1]. We also calculated time to budbreak of each tree using Eq. 2: Time to budbreak of each tree (days) = $\frac{1}{N}\sum_{i=1}^{N} DAY_i$ [Eq. 2] where N is the total number of shoot cutting replicates exhibiting budbreak and DAY_i is the incubation day with the first appearance of budbreak for each shoot cutting. Finally, for both budbreak rate and time to budbreak, we calculated the mean value for each month for the 20 trees. While both budbreak rate and time to budbreak are used for detecting the state of dormancy (e.g., Zhang et al. 2021a), budbreak rate better complies with the concept of dormancy: budbreak can not occur unless chilling is satisfied to release dormancy. Time to budbreak can strengthen the detection of dormancy, which in theory decreases as the intensity of dormancy relieves.

Measurement of Physiological and Biochemical Traits

We measured the respiration rate, contents of carbohydrates (starch, glucose, and fructose), the phytohormones (indole-3-acetic acid [IAA], abscisic acid [ABA], salicylic acid [SA], jasmonates [jasmonic acid: JA and jasmonic acid-isoleucine: JA-Ile, cytokinins [*trans*-zeatin: tZ and isopentenyladenine: iP]) in the shoots.

The respiration rates in ten of the 110 trees were measured on the afternoons of November 26 and December 25, 2022, and January 30, March 6, and March 30, 2023; the same ten trees were used on each date and they were not used for the budbreak experiment. Respiration rates were determined by measuring dark respiration rates with a portable photosynthesis system (LCpro-SD; ADC BioScientific, Hoddesdon, Hertfordshire, UK) according to Shimada (2017) with modifications (Online Resource 1). The contents of carbohydrates and phytohormones were measured in ten of the 20 trees sampled for the budbreak experiment (see section "Determination of dormancy release and growth resumption") on the afternoons of November 21 and December 25, 2022, and January 27, February 28, and March 30, 2023 (total of 50 trees). Soon after sampling, the shoots were put in a cooler bag filled with ice packs, brought to the laboratory, and stored at − 80 °C until further analysis. Contents of starch in shoots were measured using a starch quantification kit (K-TSHK; Megazyme, Bray, Wicklow, Ireland) according to the manufacturer's instructions (Online Resource 2). Sugars were extracted and their contents were quantified by high-performance liquid chromatography according to Chmielewski et al. (2017) with modifications (Online Resource 3). Phytohormones were extracted and the contents were quantified by liquid chromatography-electrospray ionization-tandem mass spectrometry according to Matsuura et al. (2019) (Online Resource 4).

Determination of Dry Weight

To calculate contents of carbohydrates and phytohormones on a dry weight basis, we first determined the ratio of fresh weight to dry weight for each tree. For each tree, shoots were milled and sieved through a 212-µm mesh into a fine powder, and 0.30 g of fine powder was scooped into a cylindrical weighing bottle (30 × 50 mm, 24 mL; AS ONE, Osaka, Japan), oven-dried at 70 °C for 48 h, after which the dry weight of the sample was measured. Finally, the fresh weight was divided by the dry weight to determine the ratio.

Statistical Analysis

All statistical analyses were conducted in R 4.3.1. (R Core Team 2023). To evaluate the degree of dormancy, changes in the rates of budbreak and time to budbreak with sampling dates were analyzed using generalized linear models of Eq. 3 and Eq. 4 respectively: Logit (Budbreak rate) = Sampling date [Eq. 3]; Log (Time to budbreak) = Sampling date [Eq. 4]. Budbreak rates were assumed to follow a binomial distribution and the logit link function was adopted in the model. Time to budbreak

was assumed to follow a gamma distribution and the log link function was adopted in the model. To determine physiological and biochemical traits, changes in the contents of carbohydrates and phytohormones with sampling dates were analyzed using generalized linear models of Eq. 5: Log (Content of carbohydrate or phytohormone) = Sampling date [Eq. 5]. For respiration rates, because the values were measured in the same trees throughout the experiment, changes in the rates with the sampling dates were analyzed using a generalized linear mixed model of Eq. 6: Log (Respiration rate) = Sampling date + (Individual tree) [Eq. 6] with the individual tree as the random effect. In these models, physiological and biochemical parameters were assumed to follow a gamma distribution and the log link function was adopted. See Table 1 for summary of models.

All of these models were subjected to Tukey's method adapted for generalized linear models and generalized linear mixed models (GLHT function in multcomp package; Hothorn et al. 2008) to assess the differences in response variables across sampling dates.

To evaluate the interrelationships of dormancy release and growth resumption with physiological and biochemical parameters, monthly means of the budbreak rate and each parameter were standardized within each variable and subjected to principal component analysis (PCA).

Results

Determination of Dormancy Release and Growth Resumption

Overall, budbreak rates were high throughout the experimental period (Fig. 3a). Even so, November had the lowest mean (± standard error) of 75.0 ± 5.4%, followed by a significant increase in December reaching 90.0 ± 3.4% ($P = 0.047$). After a slight decline in January of 86.0 ± 3.6%, the budbreak rates further increased in February reaching 97.0 ± 1.6%. The high budbreak rates continued until March (i.e., 98.0 ± 1.4%), at which time 21.0 ± 5.9% of shoot cuttings of the 20 trees showed budbreak in the plantation site in Takakuma Experimental Forest (i.e., day 0 of incubation).

Table 1 Models and its components for each response variable

Response variable	Model type	Explanatory variable	Random effect	Error distribution	Link function
Budbreak rate	GLM	Sampling date		Binomial	Logit
Time to budbreak	GLM	Sampling date		Gamma	Log
Carbohydrate content	GLM	Sampling date		Gamma	Log
Phytohormone content	GLM	Sampling date		Gamma	Log
Respiration rate	GLMM	Sampling date	Individual tree	Gamma	Log

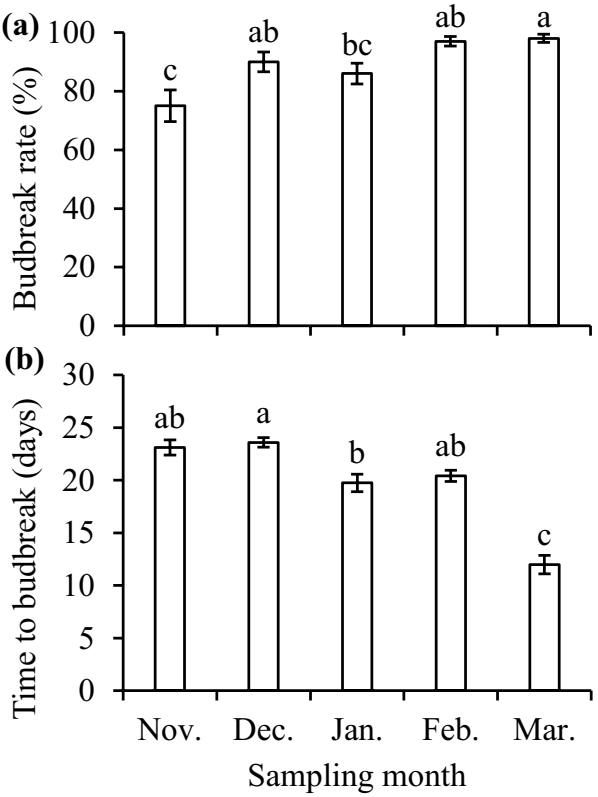


Fig. 3 Temporal changes in (**a**) budbreak rates and (**b**) time to budbreak of shoot cuttings from November 2022 to March 2023. Bars indicate standard errors. Different letters indicate significant differences among sampling months (Tukey's method; $P < 0.050$)

Opposite to budbreak rate, time to budbreak tended to shorten as winter progressed (Fig. 3b). Time to budbreak was long in November and December, at about 23.1 ± 0.7 days and 23.6 ± 0.5 days, respectively. Then, time to budbreak significantly shortened to 19.8 ± 0.8 days in January ($P = 0.027$), remained at a similar value of 20.4 ± 0.5 days in February, and again significantly shortened to 12.0 ± 0.9 days in March ($P < 0.001$).

Respiration Rates

Respiration rates were high in November at about 12.50 ± 1.35 nmol g^{-1} s^{-1}, and decreased gradually until January reaching 7.18 ± 0.93 nmol g^{-1} s^{-1} (Fig. 4). The respiration rates in January were significantly lower than in November ($P < 0.001$). The rates increased significantly on March 6 reaching 10.09 ± 1.08 nmol g^{-1} s^{-1} ($P = 0.044$), and declined again on March 30 to 7.55 ± 0.77 nmol g^{-1} s^{-1} which was significantly lower than in November ($P < 0.001$).

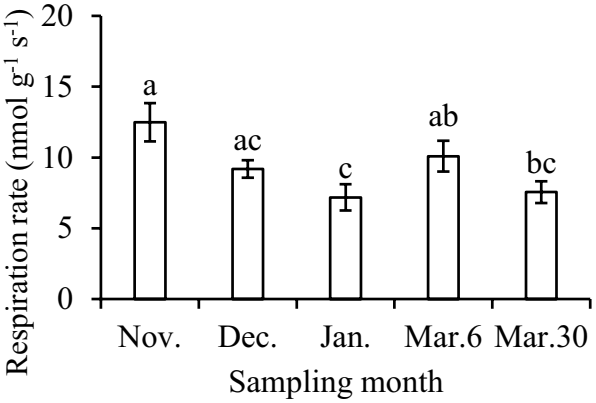


Fig. 4 Temporal changes in respiration rates of shoots from November 2022 to March 2023. Bars indicate standard errors. Different letters indicate significant differences among sampling months (Tukey's method; $P < 0.050$)

Carbohydrate Contents

The contents of starch in November (i.e., 34.1 ± 5.0 mg g^{-1}) decreased significantly in December to 22.5 ± 1.7 mg g^{-1} ($P = 0.014$), and remained low in January with a value of 19.0 ± 0.7 mg g^{-1} (Fig. 5a). The contents of starch then continued to increase significantly until March ($P < 0.001$), eventually reaching a value of 201.1 ± 22.4 mg g^{-1}.

The contents of glucose increased significantly from a value of 11.23 ± 0.33 mg g^{-1} in November, reaching a peak in January with a value of 22.76 ± 0.87 mg g^{-1} ($P < 0.001$; Fig. 5b). The contents of glucose then decreased significantly until March ($P < 0.002$), reaching a level of 12.27 ± 0.59 mg g^{-1} which was similar to that in November.

Similar to the glucose contents, the contents of fructose continued to increase significantly from a value of 16.95 ± 0.38 mg g^{-1} in November until January reaching a value of 33.16 ± 1.16 mg g^{-1} ($P < 0.001$; Fig. 5c). They remained at a high value of 33.81 ± 0.68 mg g^{-1} in February, and then decreased significantly in March to a value of 25.54 ± 0.68 mg g^{-1} ($P < 0.001$).

Phytohormone Contents

The temporal changes in phytohormone contents differed between the different phytohormones and were grouped into four patterns. The first pattern was seen for the contents of ABA and SA, which decreased during winter (Fig. 6b and c). Contents of 1395 ± 186 ng g^{-1} and 165.6 ± 15.8 ng g^{-1} for ABA and SA in November tended to decrease until February reaching values of 462 ± 41 ng g^{-1} and 76.8 ± 6.5 ng g^{-1} respectively; the decrease in February was significant for both phytohormones ($P < 0.004$). The contents of ABA and SA increased to values of 652 ± 94 ng g^{-1} and 107.6 ± 14.2 ng g^{-1} respectively in March, however, these

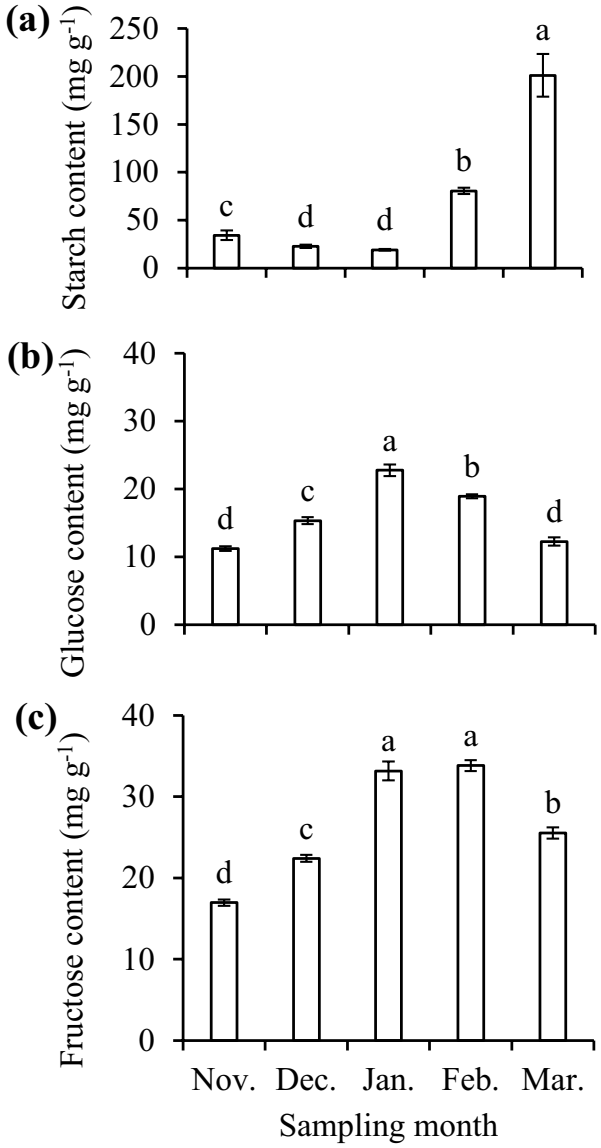


Fig. 5 Temporal changes in carbohydrate ([**a**] starch, [**b**] glucose, and [**c**] fructose) contents in shoots from November 2022 to March 2023. Bars indicate standard errors. Different letters indicate significant differences among sampling months (Tukey's method; $P < 0.050$)

increases were not significant. The second pattern was seen for the contents of tZ, which increased during winter (Fig. 6f). The contents of tZ gradually increased until February reaching 0.1491 ± 0.0112 ng g^{-1}, and this value was significantly higher than 0.0999 ± 0.0111 ng g^{-1} in November ($P = 0.037$). The third pattern was seen for the contents of IAA, JA, and JA-Ile, which increased during spring

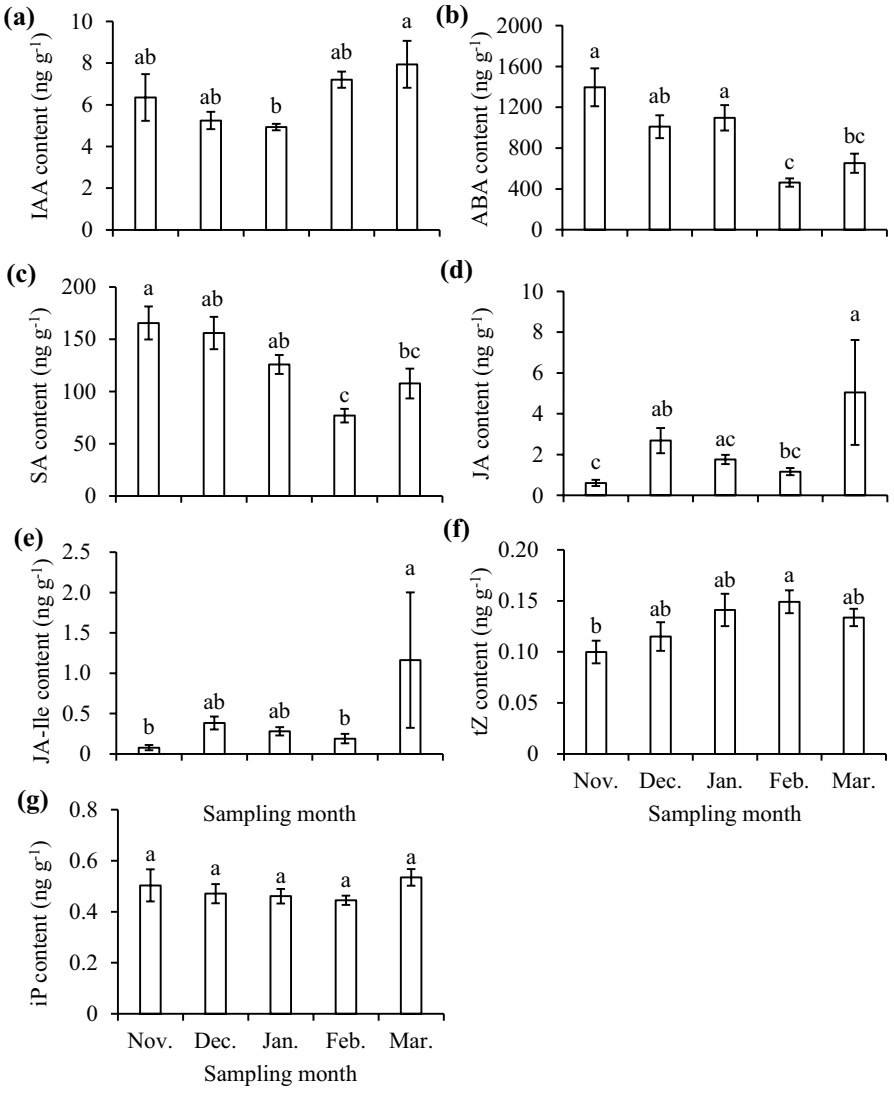


Fig. 6 Temporal changes in phytohormone ([**a**] IAA, [**b**] ABA, [**c**] SA, [**d**] JA, [**e**] JA-Ile, [f] tZ, and [g] iP) contents in shoots from November 2022 to March 2023. Bars indicate standard errors. Different letters indicate significant differences among sampling months (Tukey's method; $P < 0.050$)

(Fig. 6a, d, and e). The IAA contents increased from 4.931 ± 0.156 ng g^{-1} in January to 7.943 ± 1.121 ng g^{-1} in March, and these values were significantly different ($P = 0.020$). For contents of JA and JA-Ile, the values significantly increased ($P < 0.019$) from February (1.165 ± 0.173 ng g^{-1} and 0.189 ± 0.059 ng g^{-1} respectively) to March (5.042 ± 2.572 ng g^{-1} and 1.162 ± 0.840 ng g^{-1} respectively). The fourth pattern was seen for the contents of iP, which showed little change throughout the experimental period (Fig. 6g).

Interrelationships Among Budbreak Rates and Physiological and Biochemical Traits

PCA showed that 49.5% and 34.7% of the variation could be explained by PC1 and PC2, respectively (Table 2 and Fig. 7). The budbreak rates, respiration rates, and contents of ABA and SA were strongly associated with PC1. The budbreak rates showed a positive factor loading, whereas the three traits showed negative factor loadings. Budbreak rates showed strong correlations with contents of ABA and SA, and these two biochemical traits were strongly correlated to each other as well (Table 3). On the other hand, respiration rates showed a moderate degree of correlation with budbreak rates, and they showed less correlation with ABA and SA. Contents of fructose, tZ, starch, IAA, JA, and JA-Ile also showed positive factor loadings of PC1, and they showed moderate degree of correlations with budbreak rates ($0.5 < r < 0.8$). However, these biochemical traits were discriminated by PC2. The contents of fructose and tZ showed negative factor loadings of PC2 with a strong correlation with each other. Furthermore, the contents of starch, IAA, JA, and JA-Ile showed positive factor loadings of PC2; strong correlations were observed for starch contents with contents of IAA and JA-Ile, and for JA with JA-Ile. The contents of glucose and iP were strongly associated with PC2. The contents of glucose showed a negative factor loading, and the contents of iP showed a positive factor loading.

Table 2 Proportion of variance and factor loading of Principal Component Analysis of budbreak rate and physiological and biochemical traits

Axis of PCA	PC1	PC2
Proportion of variance	0.495	0.347
Factor loading		
Budbreak	0.604	−0.028
Respiration	−0.434	0.112
Starch	0.490	0.430
Glucose	0.146	−0.648
Fructose	0.420	−0.516
IAA	0.377	0.378
ABA	−0.582	0.091
JA	0.426	0.405
JA-Ile	0.449	0.441
SA	−0.551	0.229
tZ	0.526	−0.386
iP	0.053	0.667

*The cumulative proportion of variance explained by PC1 and PC2 is 0.842

*The reconstruction error calculated as the square root of the sum of squared differences between standardized and reconstructed values using PC1 and PC2 is 2.756

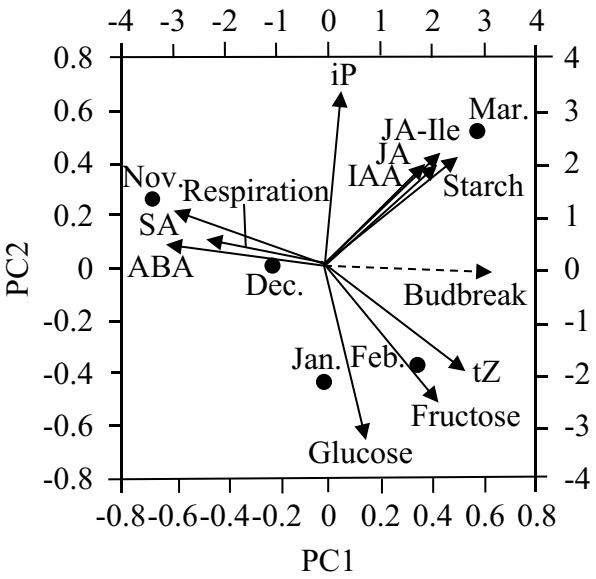


Fig. 7 Principal component analysis (PCA) on monthly changes (circles) in the budbreak rate (dashed arrow) and physiological and biochemical traits (solid arrows) with axes of PC1 and PC2

Discussion

Dormancy Release and Growth Resumption

The long time required for budbreak (i.e., 23.1 ± 0.7 days) as well as the lowest budbreak rate of 75.0 ± 5.4% in November (Fig. 3) indicated a state of shallow dormancy at this time, confirming our first hypothesis. As expected, the short time required for budbreak (i.e., 12.0 ± 0.9 days) and the highest budbreak rate of 98.0 ± 1.4% in March indicated that dormancy had been released by this time. Furthermore, the first appearance of budbreak in the field in March indicated that Japanese cedar was in the growth resumption stage in spring. Between the stages of dormancy and growth resumption (i.e., December to February), budbreak rates and time to budbreak both steadily changed, indicating that dormancy was gradually released during this time. However, the fact that budbreak rates in December were not significantly different from the budbreak rates at the growth resumption stage indicated that dormancy was almost completely released in early winter, rather than late winter as hypothesized.

Dormancy occurring in autumn in Japanese cedar seems plausible as the entrance of dormancy in autumn has been widely observed in other species (e.g., Ito et al. 2012; Kovaleski 2022; Zhang et al. 2023), and this seems the case in species with shallow dormancy as well (Zhang et al. 2021a). Furthermore, dormancy in autumn is also supported by Nose et al. (2023), reporting that Japanese cedar growing in the warm-temperate zone of Japan exhibits shoot growth until late October. The almost complete release of shallow dormancy in early winter in Japanese cedar in the warm-temperate zone may be due to a more yielding chilling requirement compared to that of species with deep dormancy (Jewaria et al. 2021; Zhang et al. 2021b): Zhang et al. (2021a) reported that air temperatures of up to 15 °C are effective in

Table 3 Correlation matrix of budbreak rate and physiological and biochemical traits. Values represent the correlation coefficient between variables. Bold indicates significant correlations ($P \leq 0.050$; Pearson correlation test)

Variables	Budbreak	Respiration	Starch	Glucose	Fructose	IAA	ABA	JA	JA-Ile	SA	tZ	iP
Budbreak	1.000											
Respiration	−0.596	1.000										
Starch	0.653	−0.338	1.000									
Glucose	0.199	−0.505	−0.411	1.000								
Fructose	0.593	−0.596	0.068	0.861	1.000							
IAA	0.509	0.095	**0.878**	−0.505	−0.007	1.000						
ABA	**−0.951**	0.391	−0.621	−0.209	−0.642	−0.619	1.000					
JA	0.634	−0.669	0.784	−0.282	0.000	0.420	−0.419	1.000				
JA-Ile	0.621	−0.615	**0.880**	−0.331	0.008	0.557	−0.446	**0.980**	1.000			
SA	−0.800	0.377	−0.521	−0.414	−0.812	−0.564	**0.916**	−0.198	−0.273	1.000		
tZ	0.748	−0.636	0.314	0.710	**0.967**	0.222	−0.790	0.194	0.221	**−0.913**	1.000	
iP	−0.051	−0.022	0.668	−0.791	−0.601	0.517	0.154	0.631	0.706	0.263	−0.422	1.000

releasing shallow dormancy. If indeed Japanese cedar has a more yielding chilling requirement, the disruption of dormancy release in this species growing in the warm-temperate zone may be negligible. Future research should investigate the chilling requirement of Japanese cedar growing in the warm-temperate zone.

Physiological and Biochemical Traits Related to Dormancy Release and Growth Resumption

Budbreak rates gradually increased over time (Fig. 3a) and were associated with PC1 (Table 2 and Fig. 7), which indicated that the process of dormancy release to growth resumption could be explained by this principal component. Respiration rates and contents of ABA and SA were also associated with PC1, showing opposite trends to the temporal changes with budbreak rates (Figs. 4, 6b, and c). This indicated that the diminishment of these physiological and biochemical traits was involved in dormancy release and growth resumption. On the other hand, compared to respiration rates, contents of ABA and SA were more strongly correlated to budbreak rates (Table 3), suggesting that the level of involvement with the process of dormancy release to growth resumption seems to be stronger in ABA and SA. In fact, high levels of ABA and SA can inhibit plant growth (Brookbank et al. 2021; Li et al. 2022; Liu et al. 2022). Furthermore, depletions in ABA are known to release dormancy (Liu and Sherif 2019), and the levels of ABA are known to be influenced by the levels of SA (Bandurska and Stroiński 2005; Szepesi et al. 2009), which also supports the strong correlation between these phytohormones in our study. In Japanese cedar growing in the warm-temperate zone, it is suggested that the depletion of ABA, which is induced by the depletion of SA, relaxes the growth repression effect, i.e., the status of dormancy, leading to the release of dormancy and the resumption of growth. However, it is noteworthy that the depletions of ABA and SA were not significant when dormancy was almost completely released, i.e., in December, which questions their significance in the early stages of dormancy release (i.e., shallow dormancy release) in Japanese cedar growing in the warm-temperate zone. As respiration rates are known to be influenced by air temperature (Atkin et al. 2005), the lower correlation of respiration rates with budbreak rates was most likely due to the recovery in respiratory activity when air temperature rose in February (Fig. 1a and b) rather than the status of dormancy.

Fructose and one type of cytokinin, tZ, accumulated in winter (Figs. 5c and 6f) and were positively associated with PC1 (Table 2 and Fig. 7). However, their correlations with budbreak rates were not as strong as that of ABA and SA (Table 3), which was most likely because of their depletions in spring. Thus, fructose and tZ are possibly related specifically to the stage of dormancy release, relieving the growth repression effect by elevating their levels over winter. In fact, cytokinins are known to promote growth in plants (Werner et al. 2001; Wu et al. 2021), and they can also accumulate during the release of dormancy (Liu and Sherif 2019). Furthermore, accumulation of cytokinins can be induced by high contents of sugars (Kiba et al. 2019; Salam et al. 2021), which supports the strong correlation between these biochemical traits in our study. In Japanese cedar growing in the

warm-temperate zone, the accumulation of fructose may trigger the accumulation of tZ, assisting the release of dormancy.

The contents of starch, IAA, JA, and JA-Ile were also positively associated with PC1 (Table 2 and Fig. 7). However, the correlations of these biochemical traits with budbreak rates were not as strong as that of ABA and SA (Table 3), since they showed an accumulation only in spring (Fig. 5a, 6a, d, and e). From this, it can be speculated that the accumulation of starch, IAA, JA, and JA-Ile are specifically involved in the resumption of growth in Japanese cedar growing in the warm temperate zone. In fact, starch and IAA are well known to promote growth in plants: starch is a carbon source for growth (MacNeill et al. 2017; Tetlow and Bertoft 2020), and IAA contributes to cell division and elongation (Fu et al. 2015; Liu and Sherif 2019; Sun et al. 2023). Moreover, our study observed a correlation of these biochemical traits, corroborating studies that show exogenous application of IAA promoting the accumulation of starch (Palacios et al. 2016; Wang et al. 2023). It is our assumption that a high IAA content induces the accumulation of starch, and IAA and starch synergistically promote the resumption of growth in spring of Japanese cedar growing in the warm-temperate zone. Jasmonates (i.e., JA and JA-Ile) are known to promote budbreak in spring (Liu and Sherif 2019), but their interrelationships with other biochemical traits have not been studied in detail. Although we cannot speculate on the relationships of jasmonates with starch and IAA, jasmonates appeared to promote the resumption of growth in Japanese cedar growing in the warm-temperate zone.

From the above, it seems that certain biochemical traits pertain to dormancy release, namely the depletions of ABA and SA, and the accumulations of fructose and tZ, while others seem to pertain to growth resumption namely, the status quo of ABA and SA, and the accumulations of starch, IAA, JA, and JA-Ile. Overall, these results are in line with our last hypothesis. However, one discrepancy was the accumulation of tZ during dormancy release and its slight depletion during growth resumption, while other growth promoting-phytohormones (i.e., IAA, JA, and JA-Ile) accumulated during growth resumption as expected.

An additional finding was that the contents of starch, fructose, tZ, IAA, JA, and JA-Ile were associated with PC2 as well as PC1 (Table 2 and Fig. 7). The contents of sugars (i.e., fructose and glucose) and tZ which showed negative values of PC2, peaked during winter (Figs. 5b, c, and 6f), whereas the contents of starch, IAA, JA, and JA-Ile, which showed positive values of PC2, showed low contents during winter (Figs. 5a, 6a, d, and e). These results mean that the different behavior of biochemical traits during winter (i.e., the stage of dormancy release) is reflected in PC2. The accumulation of sugars is known to enhance freezing tolerance (Xin and Browse 2000), and cytokinins, including tZ, have also been reported to promote freezing tolerance (Jeon et al. 2010; Shi et al. 2012). In addition, starch degradation induces the accumulation of sugars during winter (Ben Mohamed et al. 2010; Horikoshi et al. 2017; Fernandez et al. 2019). Therefore, there is a possibility that the PC2 axis reflects the degree of freezing tolerance, with lower PC2 scores associated with stronger freezing tolerance. If indeed the PC2 axis represents freezing tolerance, our results suggest that the

accumulation of sugar transformed from starch, and the accumulation of tZ synergistically enhance freezing tolerance during the release of dormancy, and that this cryoprotective effect is diminished by the stage of growth resumption.

Conclusion

This study measured several physiological and biochemical traits involved in dormancy release and growth resumption in Japanese cedar growing in the warm-temperate zone. In November, the long time to budbreak and the lowest budbreak rate of 75% indicated a state of shallow dormancy at this time. The high budbreak rates, a short time to budbreak, and the first appearance of budbreak in the field in March indicated the growth resumption stage at this time. The continuous changes in budbreak rates and time to budbreak between the stages of dormancy and growth resumption indicated that dormancy was gradually released (i.e., from December to February). Furthermore, the surge in budbreak rates in December indicated that dormancy was almost completely released in early winter. As for physiological and biochemical traits, respiration rates and the contents of ABA and SA decreased from November onward, remained low in March, and were negatively associated with budbreak rates. However, the correlations of ABA and SA with budbreak rates were stronger than that of respiration rates. It was speculated that the depletion of SA triggered the depletion of ABA which relaxed the repression effect of budbreak, i.e., promotion of dormancy release and growth resumption. Respiration rate was speculated to be influenced by air temperature rather than the status of dormancy. Partially overlapping with the temporal change of budbreak rates, contents of fructose and tZ increased until February, and the low contents of starch, IAA, JA, and JA-Ile throughout winter peaked in March. These biochemical traits seemed to be related to the release of dormancy or the resumption of growth. Taking our results into account, ABA and SA seems to be integral to the process of dormancy release and growth resumption, whereas respiration rates, fructose, tZ, starch, IAA, JA, and JA-Ile seem to be less influential.

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Declarations

Conflict of interests There are no potential conflicts of interest to declare.

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