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Effects of fertilization on radial growth of *Pinus pinea* explored hourly using dendrometers

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Abstract

Background Stone pine (*Pinus pinea*), a drought-resistant species, has significant socio-economic benefits and increasing interest for the establishment of productive plantations in several countries, especially in a climate change context. Monitoring hourly stem diameter variations contributes to the understanding of the tree-growth response to changes in environmental conditions and management. By monitoring the diameter expansion of tree stems, high-resolution band dendrometers were used to study the development of adult trees growing in a semi-arid coastal environment of central Chile under fertilized and non-fertilized soil conditions through the span of a year.

Results Short cycles (< 21 h) were few in fertilized and non-fertilized trees (6 and 4, respectively), whereas long cycles (> 28 h) occurred at a higher frequency in fertilized trees (16 vs 6). Most of the circadian cycles were regular (24 ± 3 h). The longest cycle duration (59 h) was observed in fertilized trees during spring. In all seasons, each phase of the circadian cycle, especially during the stem diameter increment phase (P3, irreversible growth), started earlier in fertilized than in control trees. P3 duration was significantly longer in fertilized than in control trees in springtime. The maximum shrinkage (P1) was observed in summer for both treatments. Stem diameter increased faster in fertilized than in control trees throughout the year, with the highest accumulation occurring in spring and the lowest in autumn. The daily variability pattern showed lower growth under high temperature across seasons.

Conclusions This study highlights the importance of fertilization in enhancing stone pine diameter growth. This cultural practice should be further explored to contribute to the mitigation of climate change effects in semi-arid environments.

Keywords Irrigation, Fertilization, Daily growth, Stem contraction, Conifer, Stone pine plantation, Climate change mitigation

Background

Stone pine (*Pinus pinea* L.) is a drought-tolerant Mediterranean species whose valued seeds, the pine nuts, have been harvested from wild and cultivated trees for thousands of years (Lim 2012). Significant socio-economic benefits of its cultivation have been reported for Turkey (Eker and Laz 2018), Tunisia (Schröder et al. 2014), Lebanon (Sattout and Faour 2017) and Europe (Awan and Pectenella 2017). The species shows an interesting growth and fruiting potential in Chile (Loewe et al. 2016) and other non-native countries, where there is an increasing interest in establishing productive plantations.

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Fertilization has well-known benefits on crop yield and fruit quality of nut-bearing species (Wani et al. 2016; Kumar et al. 2017). In stone pine, fertilization has been found to have positive effects on seedling growth in nursery (Montero et al. 2004) and initial growth after planting (Toca et al. 2014), and in cone production and quality (Calama et al. 2007; Kilci 2011; Freire et al. 2019). Fertilization also improves growth (Freire et al. 2019) and canopy efficiency (Correia et al. 2016). The species is sensitive to deficiency of micronutrients such as boron (Bento and Coutinho 2011) and iron (Malchi and Shenger 2011). Diameter growth was found to be stimulated by fertilization (Loewe-Muñoz et al. 2020); this effect is important due to the correlation between diameter at breast height (DBH, 1.3 m) and cone production (Freire et al. 2019).

However, little is known about stem diameter variability as a response to fertilizer supply at a fine temporal scale in the circadian cycle of stone pine. This information could be useful to provide cropping guidelines, since knowledge on the seasonal circadian cycle dynamics might be important to determine when fertilization will have a more positive effect on enhancing the recovery from the stem shrinkage induced by water deficit, and on boosting irreversible growth.

Stem diameter variations monitored by dendrometers have great potential to capture in situ forest productivity and sensitivity to environmental stress and are useful as early warning to detect stress thresholds in tree vitality and growth (Salomón et al. 2022). The daily dynamics of stem diameter fluctuations involve tree-related properties and external environmental conditions that influence the flow of water within the soil–plant–atmosphere continuum. In fact, an accurate measurement of stem diameter variations (SDVs) could be used to estimate sap flow (Sevanto et al. 2008), especially the stem shrinkage phase (Tian et al. 2019). SDVs result in reversible depletion and replenishment (Steppe et al. 2006) and irreversible diameter growth, with tree water status playing a key role (Zweifel et al. 2006), as observed in *Pinus hartwegii* Lindl. (Biondi et al. 2005) and in *P. sylvestris* L. (Zweifel et al. 2006). Thus, hourly stem diameter variation monitoring throughout the day during 1 year would help identify reversible shrinkage and swelling (Downes et al. 1999), and understand the tree's response to changes in environmental conditions (Deslauriers et al. 2007a; Drew and Downes 2009) and management. Understanding those responses is relevant since drought-exposed forests may be at risk of mortality. Therefore, there is a need to know tree susceptibility to environmental changes to contribute to the species performance in a context of climate change (Schäfer et al. 2019). The species adopts a strategy of drought tolerance and drought avoidance to

adapt to semi-arid coastal environment. Balekoglu et al. (2023a) explored the drought stress strategy of *P. pinea* seedlings, reporting that some provenances hold an isohydric (avoidance) while others an anisohydric (tolerance) behavior.

The information obtained using high-resolution dendrometers is useful for irrigation scheduling (Espadafor et al. 2017), crop growth monitoring (Steppe et al. 2015), site quality assessment and identification of main drivers of stem diameter growth at sub-diurnal resolution (Drew and Downes 2009). However, to date, no information is available on the intra-daily stem diameter variations in stone pine subjected to different management practices that would affect the circadian cycle (consecutive occurrence of shrinkage, recovery and increment phases). This approach may contribute to the understanding of the stone pine circadian clock seasonal variability and the impact of fertilization on this variability. Circadian clocks include self-sustained rhythms that persist despite a lack of external time cues and that remain largely constant under changing temperature conditions, being coupled to photoperiodic responses (McClung 2006), important for several development processes including growth control (Gyllenstrand et al. 2014).

The effect of fertilization on diameter growth was previously reported for horticultural crops (Brun and Tournier 1992) and stone pine (Loewe-Muñoz et al. 2020). Measuring short-term stem diameter changes and coupling them to environmental conditions is a practical approach to the understanding of stem sensitivity to management interventions and of the species-specific patterns (McMahon and Parker 2015; Coccozza et al. 2018; Zalloni et al. 2018).

We explored the scientific question of how fertilization affects the stone pine stem circadian cycle. The objective of the study was to characterize the stem circadian cycle (composed of contraction, expansion and irreversible growth), and to quantify stem cycle classes frequency across seasons in fertilized and non-fertilized adult stone pine trees in a semi-arid coastal environment. Our working hypothesis postulates that nutrient supply increases irreversible diameter growth, contributing to the species performance.

Methods

Study area and experimental trial

Data were collected from a 31-year-old stone pine plantation in Cahuil, Chile (34° 30' SL, 71° 59' WL) established on smooth hills with a sandy-loam and non-salty soil (E.C. 0.06 mmho cm⁻¹), slightly acid (pH=6.2), with low organic matter content (1.7%), at 125 m a.s.l. The genetic material of measured trees is a mix from Portugal and local sources. The plantation was thinned

20 years after establishment, with 50% of trees being cut; 10 years later, the plantation was pruned and thinned, with 65% being removed and an average density of 285 trees ha⁻¹ being left. At the start of the trial, average size of trees was 5.7 m in height, 16 cm DBH and 3.6 m of crown diameter, reflecting a lower growth than in the dry coast macrozone (Loewe et al. 2015).

The climate in the study area is Mediterranean, characterized by long dry summers and short intense winter precipitation (Table 1), with Pacific Ocean influence. Dry months, expressed as the sum of all months of the year for which the ratio between rainfall and evapotranspiration is below 0.5, are 8.6 per year. During the study period, negligible amount of rainfall was detected in November, February and May.

The trial to assess the fertilization effects was set up in 2013 and consisted of two treatments, control and fertilization. Plots (25 trees each) were arranged in a randomized complete block design with three replicates. One tree from the center of the plots was selected for hourly monitoring of stem diameter variations, accounting for six trees in total. Average DBH of sampled trees was 16.3 ± 1.2 cm.

Doses and fertilizers were determined according to soil deficiencies identified through soil analyses. Fertilizers were locally applied in two lateral strips at 5 cm depth. In spring 2013, fertilized trees received Novatec N-max (1500 g plant⁻¹), zinc sulfate (20 g plant⁻¹) and borax (60 g plant⁻¹). In the following autumn (2014), and in order to induce nutrient load (Li et al. 2016), trees received a second fertilization with triple super phosphate (350 g plant⁻¹) and carbamide (200 g plant⁻¹). In the studied growing season 2014/2015, spring and autumn fertilizations were repeated with the same products and doses, including macronutrients (nitrogen, phosphorus, potassium, calcium, magnesium and sulphur) and micronutrients (boron, iron and zinc).

Data collection

High-resolution band dendrometers (EMS DLR26A) were used to monitor tree growth continuously. Dendrometers were installed at a height of 1.3 m perpendicular to the slope, in three healthy trees for each treatment. Bark outermost loose layers (periderm) were slightly removed to allow proper mounting and to ensure close contact with the stem. The temperature-compensated electronic band dendrometers have a resolution of < 1 μm (Environmental Measuring Systems, Brno, Czech Republic). Raw data were taken every hour, stored into a data logger memory and downloaded using a converting cable with built-in infrared transceiver USB EMS/IrDA. Dendrometer temperature sensor operates on the range from -30 to 60 °C.

Stem circumference variations were recorded daily at 1-h intervals (00:00 to 24:00) from June 2014 to May 2015 using the software EMS Mini32. Changes in stem circumferences were converted to stem diameter variations assuming a circular cross-section (Vospornik and Nothdurft 2018). From dendrometers, surrounding air temperature was obtained at 1-h intervals. Main daily air temperatures, precipitation, and potential evapotranspiration were obtained and summarized by season (Table 1). The distribution of daily mean air temperature and annual precipitation is presented in Fig. 1.

Circadian cycle characterization

To study the stem circadian cycle, the hourly SDVs were accumulated and split into three different phases covering approximately 24 h (Deslauriers et al. 2007b). The contraction phase (phase 1, P1) corresponds to the stem shrinkage and is calculated as the difference between the maximum stem diameter value of the previous cycle and the minimum stem diameter value of the current cycle. The expansion phase (phase 2, P2) represents the stem swelling, and involves the period from the minimum to the maximum previous cycle stem diameter value. The stem diameter increment

Table 1 Seasonal variation in climatic variables in Cahuil (Chile) from winter 2014 to autumn 2015

Season	Air temperature ^a (°C)			Precipitation ^b (mm)	Potential evapotranspiration ^c (PET, mm)
	Mean	Minimum	Maximum		
Winter	11.4 ± 0.2	6.0 ± 0.3	21.7 ± 0.6	146.5	209.8
Spring	14.9 ± 0.2	8.0 ± 0.3	27.2 ± 0.4	20.0	476.1
Summer	17.4 ± 0.1	10.6 ± 0.2	30.7 ± 0.4	1.8	522.3
Autumn	14.4 ± 0.3	7.5 ± 0.4	28.6 ± 0.5	73.8	281.9
All year	14.5 ± 0.2	8.0 ± 0.2	27.1 ± 0.3	242.1	1490.1

^a Obtained from dendrometers; ^b obtained from DGA Pichilemu, Chile; ^c estimated from dendrometer data

Winter: June 21st–September 20th, spring: September 21st–December 20th, summer: December 21st–March 20th, and autumn: March 21st–June 20th

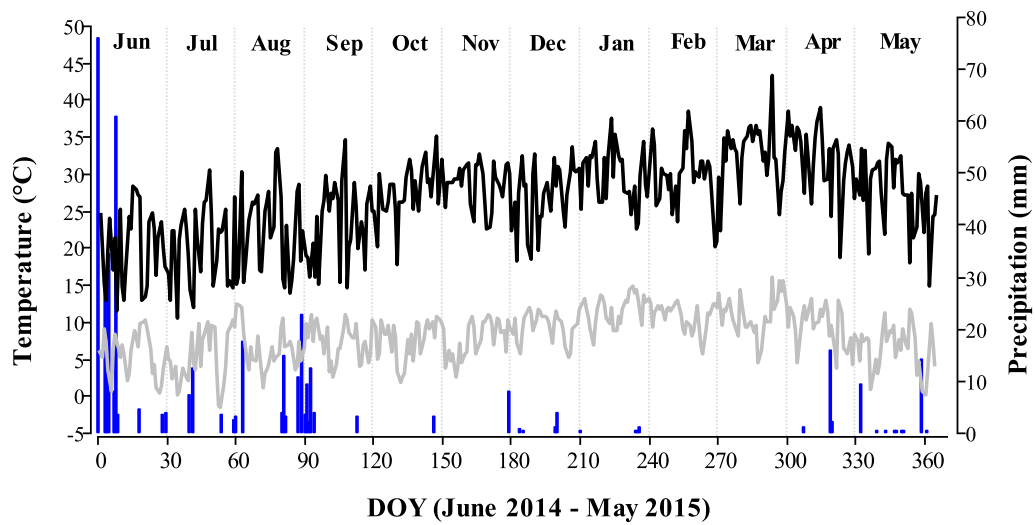


Fig. 1 Rainfall (blue), and maximum (black) and minimum (grey) air temperature during the study year

(phase 3, P3) starts when the accumulated SDV exceeds the previous cycle maximum and lasts until the next maximum (Fig. 2). The maximum cycle stem expansion (TE) corresponds to the difference between the

minimum and the maximum stem diameter value of the cycle (sum of P2 and P3).

Time of onset was determined as the start of each phase for all circadian cycles by using treatment average

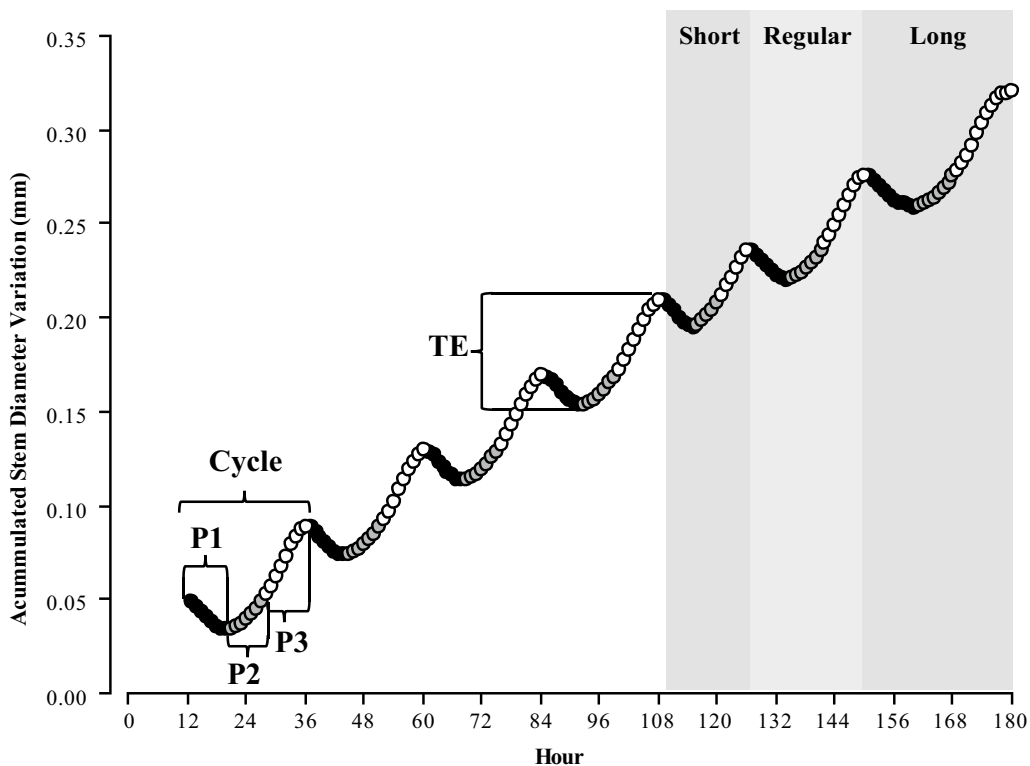


Fig. 2 Circadian cycle of stem growth studied from hourly SDVs in stone pine by phase. Each cycle is divided into three phases: contraction (P1, black), expansion (P2, grey) and stem diameter increment (P3, white). Total expansion (TE) corresponds to the maximum stem expansion of the cycle (P2 + P3). A short cycle lasts 18 h, a regular cycle lasts close to 24 h, and a long cycle up to 2.5 days

SDV series. The mean phase duration was calculated after classifying the cycles into short, regular and long duration: cycles lasting less than 21 h, 24 ± 3 h, and more than 28 h, respectively (Deslauriers et al. 2007a). To obtain the representation of SDVs throughout the year, a window of 1 month was studied in each season; seasonal mean values were calculated using all days of August (winter), November (spring), February (summer) and May (autumn). The monthly frequency of cycle types was analyzed to understand cycle distribution.

Data analyses

Both components of the circadian stem cycle study (phase duration and SDVs) were analyzed through mixed ANOVA models using the stem cycle as the unit of analysis. To compare phase duration between treatments, the ANOVA model included fixed effects of treatment, phase, season and their interactions, and a random cycle effect. Residuals from the phase duration model were normally distributed. Differences in the frequency distribution of the cycle class (short, regular and long) were χ^2 tested using marginal tables (or across seasons). All seasons were considered together in the χ^2 analysis, since the number of non-regular cycles was low.

For the second circadian stem cycle component, SDVs were studied in cycles of regular duration. The ANOVA models used to analyze the phases of contraction, expansion and stem diameter increment involved fixed effects of treatment, season and their interactions, and a random cycle effect. These parameter distributions were asymmetric; thus, data were transformed by the square root of the value + 1.5, as in Deslauriers et al. (2007a). The LSD test ($\alpha = 0.05$) was used for mean comparisons.

The empirical distribution function of SDV of cycles with data from all dendrometers during the 365 days was constructed to provide a proxy of how stem diameter accumulated throughout the year by treatment. Then, the cycle's SDVs of fertilized and control trees were correlated with hourly air temperature using the Spearman rank correlation coefficient. Statistical analyses were performed using the software Infostat (Di Rienzo et al. 2023) and its interface with the software R (R Core Team 2020).

Results

Circadian cycle timing and duration

The time of onset and duration of each phase are presented in Table 2; this table also includes the number of cycles in each circadian cycle class (short, regular and long) in 1 month by season. The number of short cycles (<21 h) was low in both fertilized and non-fertilized trees (in total, 6 and 4 in the four studied months, respectively). Long cycles occurred at a higher frequency in fertilized than in control trees (16 vs. 6 during the

four studied months). Most of the circadian cycles were regular (105 for control trees and 85 for fertilized trees during the four studied months) and lasted on average 23:57 h. The average longest cycle duration (59:00 h) was observed in spring for fertilized trees (Table 2). In all seasons, on average onset occurred earlier in fertilized trees than in the control ones, especially for P3.

Treatment \times season \times phase interactions were non-significant ($p = 0.08$) for phase length. Second-order interactions of season \times phase and treatment \times phase were statistically significant ($p < 0.01$), but treatment \times season was non-significant ($p = 0.22$). The duration of the phases of the regular circadian cycles is presented in Table 3. The contraction phase was not affected by fertilization, being similar in both treatments ($p > 0.05$) in all seasons. Fertilization showed a significant effect on the expansion phase duration, which was shorter than in control trees except in autumn. In all seasons, on average, the stem diameter increment phase lasted longer in fertilized than in control trees, with significant differences only in spring.

Stem variations during a circadian cycle

At a month scale, the number of short and long cycles in stone pine was low, whereas between 19 and 28 regular cycles per month were observed; therefore, only regular cycles were used to study stem hourly variations during a circadian cycle. Table 4 shows the mean SDVs of each cycle phase by treatment and season. For the contraction phase (P1), the treatment \times season interaction was non-significant ($p = 0.43$); the treatment effect was non-significant ($p = 0.53$), and the season effect was statistically significant ($p < 0.01$). For the stem diameter increment phase (P3), the treatment \times season interaction was significant ($p = 0.01$), as well as the treatment effect ($p < 0.01$) and the season effect ($p < 0.01$). For the total expansion (P2 + P3), the treatment \times season interaction was significant ($p < 0.01$), as well as the treatment effect ($p < 0.01$) and the season effect ($p < 0.01$).

For P1, the maximum shrinkage (highest contraction of the cycle) was observed in summer for both treatments (Table 4). The total expansion mean was statistically different between treatments in winter and spring (4.2 and 2.3 times, respectively; Table 4). P3 showed statistically higher mean values in fertilized trees than in control ones in winter and spring (Table 4). The smallest SDVs of P3 occurred in fertilized trees in autumn and in control trees in winter. The circadian cycle class frequency was statistically significant between treatments across seasons ($\chi^2 = 6.77$, $p = 0.03$) (Fig. 3).

The empirical distribution function from raw SDV data shows that stem diameter accumulated faster in fertilized than in control trees throughout the year (Fig. 4). Accumulated diameter growth during the study year was on

Table 2 Onset and duration of circadian cycle phases for fertilized and control stone pine trees

Season	Treatment	Cycle phase	Onset [h:min]	Duration by cycle class [h:min]				
				Short	Regular	Long	All cycles	
Winter	Control	All cycles <i>n</i> = 29			Short <i>n</i> = 2	Regular <i>n</i> = 23	Long <i>n</i> = 4	All cycles <i>n</i> = 29
		1	14:58 ± 0:22	3:30 ± 1:30	9:00 ± 0:43	9:15 ± 2:54	8:39 ± 0:43	
		2	23:37 ± 0:36	14:30 ± 2:30	13:37 ± 0:51	13:15 ± 4:24	13:37 ± 0:52	
		3	10:30 ± 2:10	–	8:00 ± 4:01	22:00 ± 11:00	12:40 ± 4:49	
		Whole		18:00 ± 1:00	24:00 ± 0:19	33:30 ± 3:53	24:54 ± 0:53	
			All cycles <i>n</i> = 27	Short <i>n</i> = 1	Regular <i>n</i> = 21	Long <i>n</i> = 5	All cycles <i>n</i> = 27	
	Fertilized	1	13:24 ± 0:17	2:00 ± 0:00	6:49 ± 0:38	6:12 ± 1:14	6:31 ± 0:34	
		2	19:56 ± 0:32	3:00 ± 0:00	7:37 ± 1:07	5:24 ± 2:25	7:02 ± 0:59	
		3	1:10 ± 1:01	15:00 ± 0:00	11:18 ± 1:07	30:12 ± 8:34	15:34 ± 2:31	
		Whole		20:00 ± 0:00	23:34 ± 0:15	41:48 ± 9:06	26:49 ± 2:06	
			All cycles <i>n</i> = 29	Short <i>n</i> = 0	Regular <i>n</i> = 28	Long <i>n</i> = 1	All cycles <i>n</i> = 29	
			12:33 ± 0:15	–	7:26 ± 0:28	9:00 ± 0:00	7:29 ± 0:27	
Spring	Control	2	20:06 ± 0:17	–	7:44 ± 0:33	5:00 ± 0:00	7:39 ± 0:32	
		3	3:25 ± 0:44	–	8:54 ± 0:53	15:00 ± 0:00	9:06 ± 0:53	
		Whole		–	23:47 ± 0:16	29:00 ± 0:00	23:58 ± 0:18	
			All cycles <i>n</i> = 23	Short <i>n</i> = 0	Regular <i>n</i> = 19	Long <i>n</i> = 4	All cycles <i>n</i> = 23	
		Fertilized	1	11:31 ± 0:17	–	6:22 ± 0:37	6:15 ± 1:02	6:21 ± 0:32
			2	17:52 ± 0:29	–	4:32 ± 0:34	4:00 ± 0:24	4:26 ± 0:28
	3		22:18 ± 0:30	–	13:16 ± 0:43	48:45 ± 12:06	19:26 ± 3:28	
	Whole			–	24:09 ± 0:22	59:00 ± 11:20	30:13 ± 3:20	
			All cycles <i>n</i> = 27	Short <i>n</i> = 1	Regular <i>n</i> = 26	Long <i>n</i> = 0	All cycles <i>n</i> = 27	
			11:38 ± 0:12	4:00 ± 0:00	8:51 ± 0:26	–	8:40 ± 0:28	
	Summer	Control	2	20:18 ± 0:20	14:00 ± 0:00	11:14 ± 0:32	–	11:20 ± 0:31
			3	6:27 ± 0:41	2:00 ± 0:00	5:32 ± 0:48	–	5:21 ± 0:47
Whole				20:00 ± 0:00	24:07 ± 0:15	–	23:58 ± 0:17	
			All cycles <i>n</i> = 27	Short <i>n</i> = 2	Regular <i>n</i> = 22	Long <i>n</i> = 3	All cycles <i>n</i> = 27	
Fertilized			1	10:56 ± 0:31	4:00 ± 0:00	8:22 ± 0:40	11:20 ± 1:46	8:22 ± 0:39
			2	19:18 ± 0:28	4:30 ± 0:30	8:49 ± 0:29	9:20 ± 2:54	8:33 ± 0:32
		3	3:51 ± 0:29	9:30 ± 0:30	6:25 ± 0:49	10:20 ± 2:02	7:04 ± 0:44	
		Whole		18:00 ± 1:00	23:35 ± 0:30	31:00 ± 1:00	24:00 ± 0:42	
			All cycles <i>n</i> = 28	Short <i>n</i> = 1	Regular <i>n</i> = 28	Long <i>n</i> = 1	All cycles <i>n</i> = 29	
			13:24 ± 0:15	7:00 ± 0:00	7:56 ± 0:26	9:00 ± 0:00	7:56 ± 0:24	
Autumn		Control	2	21:20 ± 0:23	13:00 ± 0:00	15:21 ± 0:33	19:00 ± 0:00	15:24 ± 0:32
			3	6:40 ± 2:36	–	7:20 ± 2:20	–	7:20 ± 2:20
	Whole			20:00 ± 0:00	24:04 ± 0:16	28:00 ± 0:00	24:04 ± 0:19	
			All cycles <i>n</i> = 30	Short <i>n</i> = 3	Regular <i>n</i> = 23	Long <i>n</i> = 4	All cycles <i>n</i> = 30	
	Fertilized		1	12:16 ± 0:27	6:00 ± 1:00	7:34 ± 0:52	15:00 ± 1:05	8:24 ± 0:50
			2	20:40 ± 0:38	11:20 ± 1:27	15:18 ± 0:58	11:45 ± 2:22	14:26 ± 0:51
		3	3:15 ± 1:07	–	10:20 ± 2:11	8:00 ± 0:00	9:45 ± 1:39	
		Whole		17:20 ± 0:40	24:13 ± 0:22	28:45 ± 0:29	24:08 ± 0:35	
			All cycles <i>n</i> = 28	Short <i>n</i> = 1	Regular <i>n</i> = 28	Long <i>n</i> = 1	All cycles <i>n</i> = 29	
			13:24 ± 0:15	7:00 ± 0:00	7:56 ± 0:26	9:00 ± 0:00	7:56 ± 0:24	

Table 2 (continued)

n number of circadian cycles. Circadian cycles are classified according to cycle length (short, regular, long)
 One month of winter (August), spring (November), summer (February) and autumn (May) was studied

Table 3 Fertilization effects on the duration [h:min] of stem circadian cycle phases in stone pine across seasons

Season	Contraction (P1)		Expansion (P2)		Stem diameter increment (P3)	
	Fertilized	Control	Fertilized	Control	Fertilized	Control
Winter	6:49±0:45 a	9:00±0:43 a	7:37±0:45 b	13:37±0:43 a	11:18±0:50 a	8:00±1:44 a
Spring	6:22±0:48 a	7:26±0:39 a	4:32±0:48 b	7:44±0:40 a	13:16±0:48 a	8:54±0:39 b
Summer	8:22±0:44 a	8:51±0:41 a	8:49±0:44 b	11:14±0:41 a	6:25±0:44 a	5:32±0:48 a
Autumn	7:34±0:43 a	7:56±0:39 a	15:18±0:43 a	15:21±0:39 a	10:20±2:00 a	7:20±2:00 a
Average	7:17±0:23 b	8:18±0:20 a	9:04±0:23 b	11:59±0:20 a	10:19±0:36 a	7:26±0:43 a

Mean ± SE. For each phase and season, different letters indicate statistically significant fertilization effects ($p < 0.05$). One month of winter (August), spring (November), summer (February) and autumn (May) was studied. Only regular cycles were considered in this calculation

Table 4 Stem diameter variations by circadian cycle phases for fertilized and control stone pine trees expressed as mm × 100

Season	Contraction		Total expansion (P2 + P3)		Stem diameter increment	
	Fertilized	Control	Fertilized	Control	Fertilized	Control
Winter	0.12±0.05 c	0.11±0.05 c	5.66±0.69 b	1.35±1.40 c	6.12±0.69 b	1.96±1.42 c
Spring	0.08±0.05 c	0.17±0.04 c	8.56±0.65 a	3.77±0.54 c	9.20±0.66 a	4.18±0.54 bc
Summer	0.35±0.05 a	0.30±0.04 ab	3.37±0.6 c	2.07±0.65 c	4.01±0.61 bc	2.54±0.66 c
Autumn	0.14±0.05 c	0.20±0.04 bc	1.38±1.63 c	2.12±1.63 c	1.53±1.64 c	2.76±1.64 bc

Contraction: maximum cycle stem shrinkage, difference between the maximum stem diameter value of the previous cycle and the minimum stem diameter value of the cycle (P1). Total expansion: maximum cycle stem expansion, difference between the minimum and the maximum stem diameter value of the cycle (P2 + P3). Stem diameter increment: stem growth cycle rate (difference between the maximum values of two consecutive cycles) (P3). Mean ± SE. By circadian cycle component, different letters indicate statistically significant differences between treatments by season ($p < 0.05$). One month of winter (August), spring (November), summer (February) and autumn (May) was studied

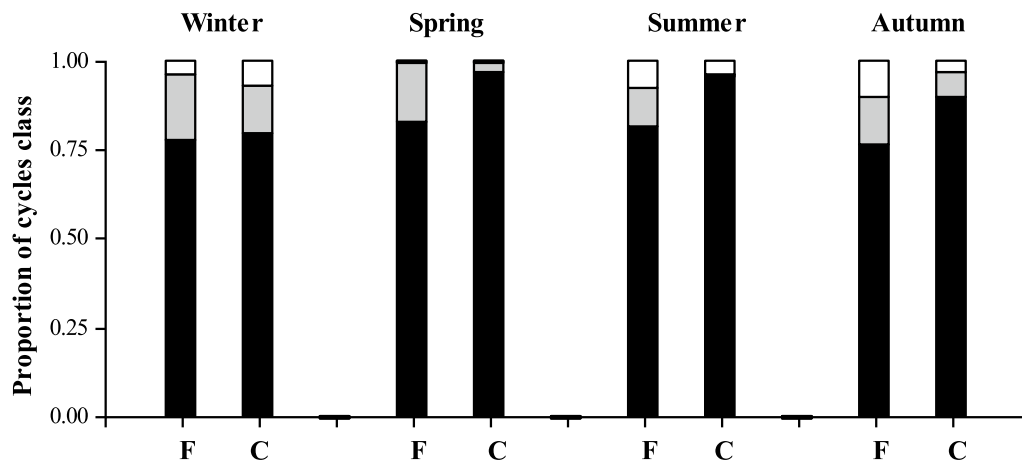


Fig. 3 Frequency distribution by circadian cycle class for fertilized and control stone pine trees. White: short; black: regular; grey: long. One month of winter (August), spring (November), summer (February) and autumn (May) was studied

average 14.9 mm in fertilized trees and 5.3 mm in control trees (Fig. 4). Time series of SDVs of the mean circadian cycle during 1 month of spring, summer, autumn and winter are shown for each treatment in Fig. 5, where P3

is highlighted. The highest and the lowest accumulated SDVs were recorded in spring and autumn, respectively, for both fertilized and control trees.

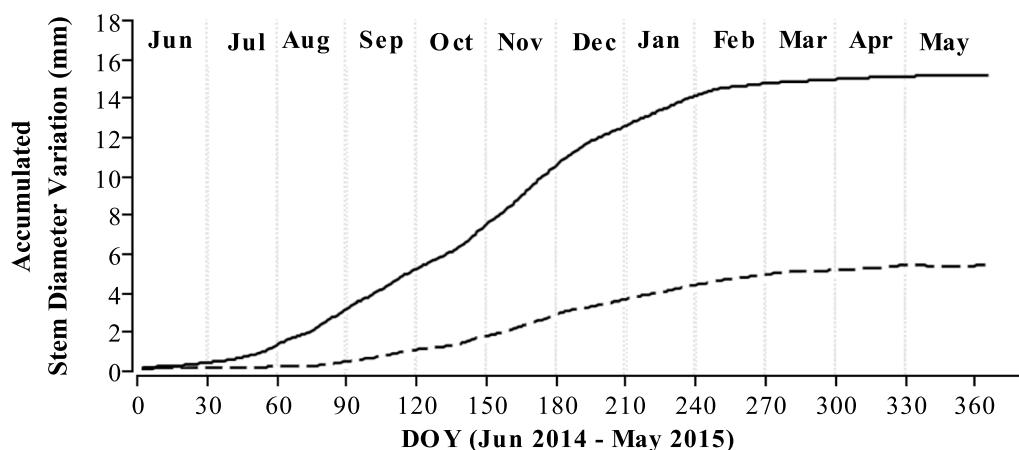


Fig. 4 Accumulated stem diameter variation during the 365-day study period by treatment. Fertilized trees (solid) and control trees (dashed)

Figure 6 presents the hourly SDV, which shows the intra-cycle stem variation, and air temperature, which was simultaneously recorded by dendrometers during 1 month in each season. A Spearman correlation was found between treatments and air temperature ($\rho = -0.60$, $p < 0.01$ for fertilized trees and $\rho = -0.43$, $p < 0.01$ for control trees) throughout the year and in every season (Fig. 6). A significant correlation between series of control and fertilized trees was also observed across seasons ($\rho = 0.74$, $p < 0.01$). The observed temporal variability pattern shows low growth under high daily temperatures in all seasons. During the fastest growth period (spring), the highest SDV values of the circadian cycle were found under fertilization treatment. Growth of fertilized trees stopped at noon and resumed at 16:00 pm, whereas in control trees, growth also stopped at noon but resumed at 20:00 pm. Irreversible growth on average started with air temperature over 11.8 °C in control trees and 10.9 °C in fertilized trees.

Discussion

Characterizing stem growth at an intra-daily scale is useful to understand the effects of management on growth. Indeed, the SDV distribution and frequency should be interpreted as a function of the physiological status of trees, which changes over the seasons (Deslauriers et al. 2007a). Seasonal SDVs can help elucidate the relationship between tree growth and seasonal climatic conditions.

The importance of characterizing the duration of the circadian cycle phases has been highlighted for other species (Deslauriers et al. 2007b). In our study, in both treatments most of the circadian cycles lasted around 24 h (regular), meaning that circadian rhythm, temperature and light are intertwined in trees, whereas the number of short and long cycles was low. Long

cycles were 2.7 times more frequent in fertilized than in control trees, indicating a longer duration of irreversible growth in managed trees; long cycle duration indicates a decoupling of growth with daily changes in temperature or light. P1, the daily shrinkage related to changes in tree moisture content, typically occurred in the afternoon in both treatments, when transpiration is higher than root water uptake (Tian et al. 2019) and stems lose water from elastic tissues (bark, cambium and immature xylem) (Zweifel et al. 2014). P1 also included the night in control trees in winter, and mornings in fertilized trees in summer. The longest P1 lasted 17 h in control trees and occurred in winter, whereas in fertilized trees it lasted 18 h and occurred in summer and autumn; these maximum durations are much shorter than the maximum P1 duration reported for *Cedrus libani* A. Rich. and *Juniperus excelsa* M. Bieb., which ranged from single days to several weeks (Güney et al. 2020). *Juniperus* species (Douaihy et al. 2013) and *Cedrus libani* can adapt to extremely harsh environmental conditions, including drought (Messinger et al. 2015). *P. pinea*, an isohydric species able to tolerate drought through different physiological mechanisms, including root mortality, stomata control and biomass allocation (Oliveras et al. 2003), showed a best performance under more intense drought than these well-known drought-resistant species. Swelling (P2), which reflects the daily water uptake that takes place after P1, occurred in nights and mornings in winter and autumn, and mostly in nights of spring and summer, both in fertilized and control trees.

The onset of the phases of the circadian cycle differed between treatments, occurring earlier in fertilized trees than in the control ones, especially for P3 (over 2.5 h earlier). Thus, fertilization reduced the influence

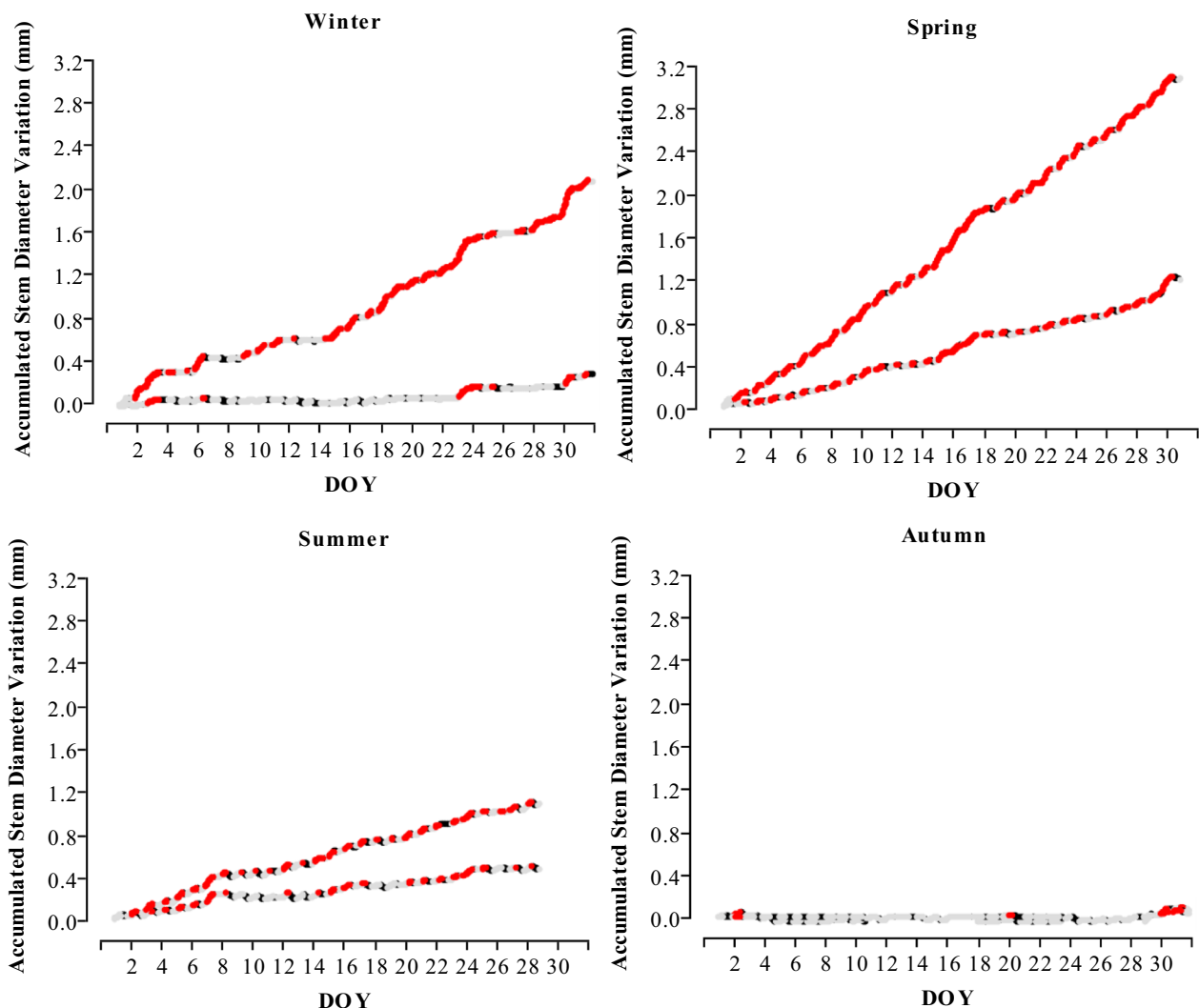


Fig. 5 Time series of circadian cycles by season and treatment (Fertilization, upper line; control, bottom line). The stem cycle is divided into three phases: contraction (solid black), expansion (grey), and diameter increment (red). One month of winter (August), spring (November), summer (February) and autumn (May) was studied

of environmental control on the phase onset reported by Oberhuber et al. (2014), in particular by air temperature, throughout the year. In a study on *Pinus cembra*, the onset of P1 and P2 in non-fertilized trees was similar to the one found in this work, and onset of P3 in summer was earlier than our values, with longer duration of the cycles and of each of the three phases (Deslauriers et al. 2007b). The asynchronous end of P3 observed between treatments suggests dependence on climatic variables (Swidrak et al. 2011), as well as an environmental control.

Phase duration could be highly impacted by climate variability, since shrinking and swelling are caused by the tree transpiration and sap flow (Perämäki et al. 2001; Tian et al. 2019). Regarding the seasonal variations in SDV patterns, fertilization reduced P1 length in summer by

over 2 h and P2 length in all seasons, except in autumn. Fertilization increased the duration of P3 in spring, influencing the effective irreversible growth duration. These positive effects of fertilization on stem diameter growth are consistent with previous results on the effect of P and P+N supply on *P. sylvestris* and *Picea abies* (Niederberger et al. 2019); in adult stone pine plantations, N was found to be the most limiting element (Rapp et al. 1979). Different species show varied responses to water deficit. In fact, *Picea abies* and *P. cembra* show a water saving behavior while *Larix decidua* maintain a relatively high transpiration even under moderate water deficit (Anfodillo et al. 1998). In particular, *P. abies* was reported to have a limited capacity to restore internal water reserves (Knüver et al. 2022). In our study, in untreated trees, P2

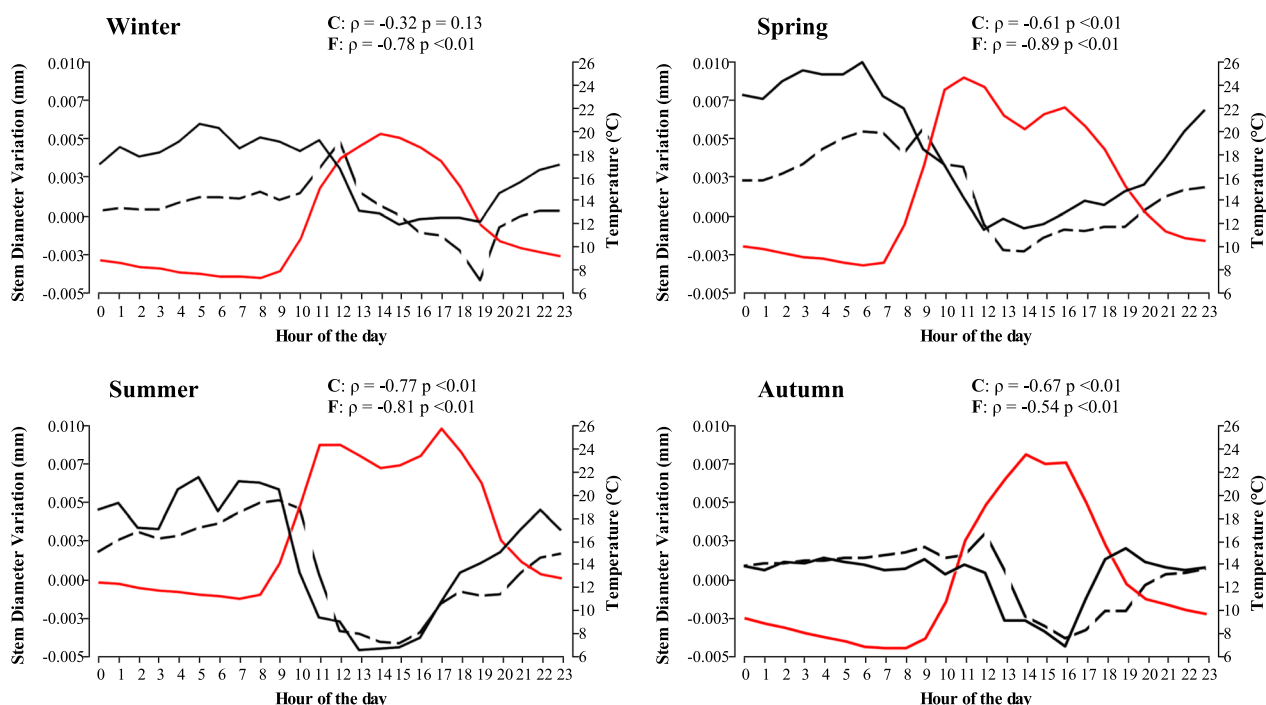


Fig. 6 Time series of hourly diameter variations and concomitant air temperature (red) by season and treatment. Fertilized trees (F): solid, control trees (C): dashed. Correlation values among SDVs and temperature series are reported in the embedded tables. One month of winter (August), spring (November), summer (February) and autumn (May) was studied

lasted 11:14 h in summer, a similar duration to the one reported for *L. decidua*, *P. abies*, *Pinus cembra* (Deslauriers et al. 2007b), and *Abies balsamea* (Deslauriers et al. 2003) in wet spring–summer, indicating a remarkable recovery of stone pine even under arid conditions.

Despite rainfall and air temperature seasonal variations, interestingly, our study showed from winter to summer that fertilization contributed to a faster recovery from the stem shrinkage induced by water deficit than observed in control trees (gains of 4:29 in winter, 3:12 h in spring and 2:40 h in summer); in spring, the fertilization impact led to a recovery phase shorter than the previous shrinkage. These results are in agreement with Balekoglu et al. (2023b) who found that in stone pine seedlings, a low C/N ratio in stems have superior resistance and recovery in summer. In the same season, in *P. taiwanensis* under high temperatures and low rainfall, the strong transpiration amplified the magnitude of contraction within tree stems; thus, the refill of the stem hydraulic capacitance was restricted due to the low soil water availability, resulting in the shrinkage of stems and lower growth and shorter duration of stem increments (Liu et al. 2018). The maximum duration of P2 indicates that fertilization induced a faster recovery (18.2% in winter, 25.0% in spring, and 6.7% in summer). This valuable finding agrees with results obtained by several

authors that point out that a sufficient nutrient supply can increase the water-use efficiency during droughts and enable a faster recovery afterwards (Gessler et al. 2017). In particular, Balekoglu et al. (2023b) found that N availability increased stone pine recovery in summer; Chambi Legoas et al. (2023) reported positive effects of K fertilization on *Eucalyptus grandis* for growth recovery following drought; and Wang et al. (2022) concluded that fertilization can alleviate the negative effects of extreme drought on survival and recovery growth of *Quercus pubescens* saplings.

In conifers, P3 is determined by soil water availability and atmospheric vapor pressure deficit (VPD) (Zweifel et al. 2005). In summer and autumn, P3 occurred mostly during the mornings in control trees, and during the nights and mornings in fertilized trees. In winter, in control trees P3 started in the morning and ended at night, whereas in fertilized trees it started during the night and finished the next afternoon and lasted three more hours. In spring, the fastest growth period when temperature is favorable for growth, P3 occurred during nights and mornings in control trees, a longer period than reported for *P. palustris*, *P. radiata* and *P. resinosa* (Mencuccini et al. 2017), and during night, morning and afternoon in fertilized trees,

a longer period than in the control trees. Thus, fertilization increased P3 duration, in agreement with our hypothesis.

The fastest stem diameter growth was observed in spring, followed by winter; in summer growth was very low, as reported for most species (Sánchez-Costa et al. 2015), due to the harsh environmental conditions during the summer drought (Liu et al. 2018). In autumn, it was negligible, probably due to low temperatures and water deficit (Aldea et al. 2021), and to the photoperiod impact, with shorter days inducing growth cessation (Gyllenstrand et al. 2014). During dry periods, even a low rainfall event ($< 15 \text{ mm day}^{-1}$) can alleviate water deficit, inducing an enlargement of the xylem cells (Zweifel et al. 2006). Mediterranean climate usually leads to a bimodal growth pattern with peaks before and after summer (Aldea et al. 2018), but in our study, trees grew before and during the dry period, probably supported by the humidity from the Pacific Ocean. In fact, the wetting of leaves with fog and dew positively affects plant water balance, without significantly increasing soil wetness (Limm et al. 2009). The studied stone pine trees grew all year round, except in autumn; thus, the growth period was much longer than that reported for *P. sylvestris* trees growing at a xeric site with higher annual rainfall, which only grew during a short period in spring (Oberhuber 2017).

Fertilization effect on irreversible growth was greatest in spring. Stem growth has been enhanced by macronutrients (Ferrer et al. 2004) and micronutrients (Schlatter and Gerding 1984a, b) availability in several pines. Species-specific responses to the nitrogen supplementation on xylem growth have been reported in *Quercus* species (Yu et al. 2019). The strongest effect of fertilization was observed in spring, when growth rates are highest (Gruber et al. 2010); this result indicates that fertilization is a useful silvicultural tool to cope with the limiting environmental conditions prevailing in the study area, e.g., drought in spring combined with a limited soil water holding capacity and nutrient deficiency. The occurrence of most irreversible growth during dry periods could be attributed to water reserves stored in the trees (Oberhuber 2017; Szymczak et al. 2020) or to the ability of stone pine to tap water from deep soil layers (Brito et al. 2017); if this ability is limited, severe drought may reduce growth and cause mortality. In fact, Schönbeck (2019) concluded that a low-intensity drought stress could be offset by increased nutrient availability, with fertilization improving the metabolism and functioning of the roots, and C allocation to belowground tissues, as also reported by Balekoglu et al. (2023b).

Understanding how daily stem growth is affected by environmental conditions provides a useful approach to the study of the variations in broadleaves (Deslauriers et

al. 2007a) and *Pinus sylvestris* (Thaabet et al. 2009) tree growth. In fact, an increase in air temperature shortened both duration and SDVs in both treatments and all seasons. This result partially agrees with findings of Deslauriers et al. (2007b), who reported its effect only on shortening duration, and disagrees with those of Oberhuber and Gruber (2010), who stated that air temperature had no influence on stem increment. The observed negative effect found in this study is probably due to the impact of transpiration on diameter growth (Tardif et al. 2001); however, contrasting effects of temperature on SDVs may occur in the circadian cycle phases, possibly associated with optimum temperature (Oladi et al. 2017) for the different physiological processes.

Temperature is a determinant of growth that was found to influence cell production in several European conifers (Rossi 2003), a positive correlation with stem diameter contraction was reported in the native *Fitzroya cupressoides* (Urrutia-Jalabert et al. 2015). Thus, growth–temperature relationships are interesting to understand growth processes and environmental drivers. Negative correlations were found in our study between SDVs and air temperature, with high temperatures reducing stem growth duration and magnitude, probably through a metabolic alteration, especially changes in leaf transpiration (Oberhuber et al. 2014). In fact, temperature above a certain threshold (16 to 21 °C) (Beedlow et al. 2013) increases photorespiration (Lewis et al. 1999), inducing a reduction in net photosynthesis, and consequently resulting in a negative effect on stem diameter growth.

The growth–air temperature correlations found at an intra-daily scale highlight the relevance of water availability on circadian cycles. The negative correlations evidenced between stem diameter increments and mean air temperature in both treatments and all seasons, except in winter, for control trees, disagree with results reported by Akkemik (2000). These negative correlations can be attributed to the water deficit caused by warm temperatures (Bachtobji-Bouachir et al. 2017), which drives changes in leaf transpiration (Oberhuber et al. 2014); transpiration is lower in *P. pinea* than in *Citrus sinensis* and *Olea europaea* (Rana and Ferrara 2019).

The effect of rainfall on stem growth and circadian cycles has been repeatedly reported as important (Tardif et al. 2001; Deslauriers et al. 2003, 2007b; Oberhuber and Gruber 2010; Oberhuber 2017; Camarero and Rubio-Cuadrado 2020; Ma et al. 2021). However, we did not study this variable because no rainfall occurred in the studied months of spring, summer and autumn, and only few events were recorded in winter (see Fig. 1). In fact, the observed ability to grow during dry periods is an indication of the species' drought tolerance (Güney et al. 2020).

Since stem growth is influenced by climatic characteristics across years (Oberhuber and Gruber 2010; Liu et al. 2018), long-term studies including the combined action of air temperature and other environmental factors should be conducted to understand the stone pine circadian cycles inter-annual variability.

Overall, the results suggest that stone pine has seasonal growth, which would be driven mainly by temperature. Interestingly, stone pine maintained a low continuous diametric growth even during the dry summer period, confirming its exceptional drought tolerance. Our results indicate a high adaptation of stone pine to current climate conditions in coastal central Chile, tolerating prolonged droughts during spring and summer. Therefore, the species would hold a promising potential for establishing productive plantations under a changing climate, which should be confirmed in future studies. This study provides additional evidence about the effects of climatic factors on stem growth, and on the importance of the availability of nutrients in the potential enhancement of irreversible growth, the most important phase of the circadian cycle from a productive point of view. Differences in nutrient acquisition may drive differential physiological processes that modify the circadian cycle of stone pine throughout the seasons. The capacity of stone pine to adjust cambial activity to environmental conditions represents an interesting strategy under climate change.

Considering the projected effects of climate change, especially in Mediterranean regions, which may reduce the species' survival capacity, studies including tree mortality are needed (Güney et al. 2020) especially under drought conditions. This knowledge is important to understand the vulnerability of productive plantations and to estimate their carbon sequestration capacity. Long-term monitoring of the fertilization effects on stem growth can contribute to the definition of climate-adaptive silvicultural strategies to promote stone pine adaptation to challenging environmental conditions, addressing limitations of this study, such as the inclusion of only one plantation, and evaluating more trees and during a longer span time to determine long-term treatment and environmental effects, such as concurrent drought.

Conclusions

The intra-daily monitoring of stem diameter variations allowed us to explore the stone pine stem circadian cycle in detail and to quantify the impact of fertilization on diameter growth. Thus, we were able to elucidate tree responses to environmental conditions. Fertilized trees exhibited a faster recovery from the shrinkage phase and a higher irreversible stem

diameter growth than control trees. SDVs can be used to assess the environmental sensitivity of forest trees to climate and management practices; this information is useful to make climate-adapted forest management decisions. Data obtained on a daily basis and with a high temporal resolution revealed a positive significant silvicultural effect of fertilization on stem diameter growth and its distribution and duration. Fertilization changed the diel pattern of growth. Indeed, in control trees irreversible growth was concentrated in nights and mornings of the fastest growth period (spring), whereas in fertilized trees, growth also occurred during the day. Thus, fertilization extended the growth period.

Irreversible diameter growth was limited by climatic stress (dry winter and hot summer), and absent in autumn, probably due to temperature above an optimum threshold and drought stress in mid-late growing season. Superior irreversible stem diameter growth was observed in spring, when temperature is favorable for growth, being fertilization effective to further increase it. The seasonal shifts detected in the stone pine circadian cycle suggest the importance of long-term monitoring growth at a daily scale, to forecast growth responses to climate variability that could be useful to make climate-adapted forest management decisions.

Abbreviations

P1	Stem diameter contraction phase, phase 1
P2	Stem diameter expansion phase, phase 2
P3	Stem diameter increment phase, phase 3
TE	The maximum cycle stem expansion
DBH	Diameter at breast height (1.3 m)
SDV	Stem diameter variation
VPD	Vapor pressure deficit
PET	Potential evapotranspiration

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Author contributions

VL, CDR and MB contributed to the study conception and design. Material preparation and data collection were performed by RDM. MB directed the statistical analyses. CDR assisted in bibliography revision. VL wrote the first draft of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets supporting the conclusions of this article are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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