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Longitudinal Growth Patterns and Climate Responses of *Larix olgensis* Trees Differing in Size and Survival Status

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Abstract

Growth decline before tree death has attracted increasing attention under climate change and plantation ageing. However, most previous studies have relied on diameter at breast height (DBH) or tree-ring measurements at breast height and have given limited consideration to longitudinal variation along the stem. Using multi-height tree-ring-width data from a *Larix olgensis* A. Henry plantation in the Wanda Mountains, we compared radial growth, annual volume increment (AVI), and seasonal climate responses among small living trees (SL), large living trees (LL), and dead trees (DT). LL maintained greater TRW than SL across all sampling positions and greater BAI than both SL and DT across relative stem heights, whereas no significant BAI difference was detected between SL and DT. Recent TRW trends declined at several relative heights in SL and DT, whereas the decline was weaker in LL. AVI trajectories peaked earliest in DT and latest in LL; mean net AVI change differed among groups ($\eta^2 = 0.428$), remaining positive in LL but negative in SL and DT. LL exhibited a coherent negative temperature response across stem positions, whereas the DT association was concentrated at 75% stem height. Together, multi-height TRW, BAI, and AVI identified sustained whole-stem growth as the defining feature separating LL from SL and DT. These findings identify longitudinal stem variation as a key dimension of growth histories and climate sensitivity among trees differing in size and survival status.

Keywords: *Larix olgensis*; longitudinal growth; annual volume increment; climate response; tree mortality

1. Introduction

Increasing evidence shows that climate change is associated with reduced tree growth and extensive forest mortality worldwide [1–3]. Plantations are a major component of global forest resources and play important roles in timber production, carbon sequestration, and ecological restoration. Their growth decline, mortality risk, and productivity stability have received increasing attention as warming and extreme climatic events intensify [4–7]. Tree mortality in plantations has important consequences for timber yield, biomass, carbon storage, and biodiversity. Background mortality is influenced by ontogeny and competition, and its risk may be exacerbated under climate change [8,9]. Tree death is usually not an instantaneous event but is associated with prolonged growth decline, water stress, altered carbon balance, and accumulated competitive pressure [3]. Pre-mortality radial-growth decline has therefore been recognised as an important early signal of mortality risk [10]. Many studies have relied on partial datasets or focused on episodic disturbances, such as severe drought, wildfire, or silvicultural treatment, whereas continuous long-term mortality dynamics remain insufficiently understood [11]. Tree rings provide continuous



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records of growth and have been widely used to analyse long-term growth variation and climate responses [12,13]. Although radial growth is commonly assessed using tree rings at breast height, such measurements represent growth at a single stem position. With increasing tree height, path length and gravitational effects may make upper-stem growth more responsive to external conditions [14–17]. Consequently, breast-height growth alone may not fully capture longitudinal growth variation or responses to environmental change at the whole-tree scale.

Radial growth varies along the stem because crown proximity, carbon allocation, hydraulic transport, mechanical loading, and stem taper change with height [18–20]. In central German beech stands, competition reduction altered the timing and magnitude of radial increment differently at the stem base and crown base [21]. In Sitka spruce plantations in Great Britain, wind exposure promoted basal reinforcement and increased stem taper [22]. Breast-height rings therefore represent one component of a longitudinal growth system, providing a direct rationale for examining growth at multiple stem positions. Tree size further affects how ring width is translated into basal-area and volume growth. Long-term Central European experiments show that size–growth relationships change with site quality, drought, and competition [23]. Analyses tracing drought effects from trees to stands likewise show that growth responses can differ across levels of organisation [24]. A Turkish tree-ring study across contrasting climatic conditions further shows that climate–growth relationships vary among regional environments [25]. Integrating multi-height TRW with BAI and AVI therefore distinguishes local cambial growth, size-related area production, and whole-tree growth history.

Larix olgensis is an important plantation species in northeastern China and contributes substantially to regional timber production and forest ecosystem functions. Research on its growth has expanded from analyses of individual climatic drivers to integrated assessments of provenance, age, competition, site conditions, and management. Radial growth and its responses to temperature and precipitation differ among provenances and test sites, indicating joint regulation by genetic background and environment [26]. In northeastern *Larix olgensis* plantations, age and competition are important controls on radial growth, while growing-season water conditions, previous-year precipitation, and thinning also influence individual growth [27]. Growth trajectories and responses to climatic warming are further related to xylem hydraulic traits [28]. Studies from the Changbai Mountains and other mountainous regions of northeastern China show that radial growth varies with temperature, precipitation, elevation, and slope position [29–32]. These studies provide regional context, although their climatic and topographic settings differ from those of the Wanda Mountains. Nevertheless, most studies have focused on breast-height or single tree-ring series, with comparatively little attention to growth at different stem heights. Radial growth may vary along the stem because of differences in crown structure, water transport, and carbon allocation [18,19]. Compared with tree-ring measurements at a single height, multi-height disc data provide a more comprehensive representation of tree growth and can be used to estimate annual volume increment or biomass growth [31,33]. Such data are particularly useful in plantations for identifying growth differences among diameter classes at different stem positions and for evaluating whether dead trees exhibit height-specific growth decline before death. Tree size and competitive status can alter hydraulic structure, rooting depth, stomatal regulation, and carbon reserves, thereby modifying sensitivity to climatic stress [5,34]. Tree size and survival status are therefore closely associated with variation in growth trajectories and climate responses. However, it remains unclear how position-specific TRW, size-related BAI, and whole-tree AVI are coordinated among living trees of different sizes and standing dead trees, and whether their climate responses vary along the stem.

The study aimed to determine how tree size and survival status were associated with longitudinal and whole-tree growth in a 44-year-old *Larix olgensis* plantation. The objectives were to: (1) compare recent TRW and BAI among SL, LL, and DT across stem positions; (2) reconstruct their whole-tree AVI trajectories and pre-death growth changes; and (3) examine whether seasonal climate responses differed among tree groups and stem positions. Accordingly, the study addressed three research questions: How did radial growth vary along the stem among the three groups? Did position-specific growth patterns correspond to whole-tree volume-growth trajectories? Did seasonal climate sensitivity exhibit a longitudinal structure?

2. Materials and Methods

2.1. Study Area

The study was conducted at the Mengjiagang Forest Farm in Jiamusi, Heilongjiang Province, China (130°32′42″–130°52′36″ E, 46°20′16″–46°30′50″ N). The area lies on the western foothills of the Wanda Mountains and is characterised by low mountains and hills with relatively gentle terrain. Mean elevation is approximately 250 m, terrain generally declines from northeast to southwest, and slopes are mainly 10–20°. The region has an East Asian continental monsoon climate, with a mean annual temperature of 2.7 °C, extreme maximum and minimum temperatures of 35.6 and −34.7 °C, respectively, mean annual precipitation of approximately 550 mm, annual sunshine duration of approximately 1955 h, and a frost-free period of approximately 120 days. Dark brown forest soils predominate, together with albic dark brown forest soils and smaller areas of gleyed dark brown forest soils, meadow dark brown forest soils, albic soils, meadow soils, marsh soils, and peat soils. Mengjiagang Forest Farm is a major base for larch plantation establishment and management and represents a typical temperate forest environment in northeastern China. The study stand was a pure *L. olgensis* plantation established in 1978 and clear-cut in 2022. At harvest, the stand was approximately 44 years old and had relatively uniform site conditions, making it suitable for multi-height stem analysis of growth.

2.2. Climate Data

Climate data were obtained from the CRU TS v4.07 monthly high-resolution gridded multivariate climate dataset, maintained jointly by the Climatic Research Unit (CRU), University of East Anglia, Norwich, UK, and the National Centre for Atmospheric Science (NCAS), Leeds, UK [35]. The dataset covers global land areas excluding Antarctica at a spatial resolution of 0.5° × 0.5° and provides continuous monthly climate records from 1901 to 2022. CRU TS data are derived from observations at meteorological stations and are quality controlled, homogenised, and spatially interpolated. Potential evapotranspiration (PET) is calculated using the Penman–Monteith formulation from temperature, vapour pressure, cloud cover, wind, and related variables.

Monthly climate data for the grid cell corresponding to the study site (46.43° N, 130.71° E) were extracted for 1990–2021. Variables included precipitation (PRE), mean temperature (TMP), maximum temperature (TMX), minimum temperature (TMN), vapour pressure (VAP), and PET.

Based on the growth phenology of *Larix olgensis* and established dendroclimatic seasonal-correlation frameworks, monthly data were aggregated into ecologically meaningful windows: the previous growing season (June–September), previous autumn (September–October), previous December, current spring (April–May), current June, and the current growing season (May–September). Temperature variables were averaged within each window, precipitation was summed, and PET and VAP were averaged.

The period used for climate-response analyses was matched to the comparable period of the TRW chronologies.

2.3. Sample-Tree Collection and Classification by Size and Survival Status

During clear-cutting in 2022, all sampled *L. olgensis* trees were surveyed for diameter at breast height (DBH, measured at 1.3 m), survival status, and stem-sampling information. To compare longitudinal growth in relation to tree size and survival status, 70 representative complete stems were selected, comprising 60 living trees and 10 standing dead trees. The sampled trees were assigned to three groups based on DBH and survival status: small living trees (SL), large living trees (LL), and standing dead trees (DT). Living trees were classified by DBH as small living trees (SL) and large living trees (LL). Their observed DBH distribution contained a gap between 14.20 and 15.01 cm; accordingly, 15 cm was used as the threshold: SL comprised living trees with DBH ≤ 15 cm, and LL comprised living trees with DBH > 15 cm (Table 1). Dead trees were classified independently as DT according to mortality status. The final sample included 30 SL, 30 LL, and 10 DT. The selected trees covered the principal DBH range and survival states within the stand and represented the major growth differences among large living, small living, and dead trees. Sample trees were selected using a stratified approach based on size class and survival status. Living trees were selected separately from small and large diameter classes (30 trees each), and 10 standing dead trees with intact main stems and apices were selected as a separate group. Specifically, the 10 standing dead trees constituted a sampled subset rather than an exhaustive collection of all dead wood in the stand. To ensure the accuracy of the relative-height standardizations, the integrity of the stem apex was strictly assessed prior to sampling; only standing dead trees with completely intact main stems and apices were included, while those with broken tops were explicitly excluded. Furthermore, the exact year of death for these standing dead trees was reliably determined based on continuous annual field monitoring and surveys of the stand, thereby minimising the temporal uncertainty associated with determining mortality.

Table 1. Basic information for the sampled tree groups.

Tree Type	Group Name	Number (Trees)	DBH Range (cm)	Mean DBH (cm)	Tree Height Mean (m)	Tree Height Range (m)
Small living trees	SL	30	7.74–14.20	10.89	14.13	5–20
Large living trees	LL	30	15.01–26.11	18.22	18.43	4–22
Dead trees	DT	10	7.90–14.00	10.76	13.60	5–16

2.4. Stem-Disc Sampling and Tree-Ring-Width Measurement

After felling, discs were collected at 1 m intervals from the stem base (0 m) to the upper stem (Figure 1e). The number of discs differed among trees because of variation in tree height. The final analytical dataset contained 63 trees (29 SL, 24 LL, and 10 DT), with 5–23 valid sampled-disc heights per tree. Discs were air-dried, progressively sanded, and scanned. Ring boundaries were identified following standard dendrochronological procedures [36]. Ring widths were then measured in the east, west, south, and north directions using Image-Pro Plus 6.0 (Media Cybernetics, Inc., Silver Spring, MD, USA).

Measurements were made to 0.01 mm, and the mean of the four directional measurements was used as the annual ring width for each cross-section.

Rings were numbered sequentially from the pith outward. Calendar years were assigned by back-calculation: the outermost ring of living trees was assigned to 2022, whereas the outermost ring of each dead tree was assigned to its recorded year of death. Thus, recent-growth analyses used tree-specific outermost 15-ring windows aligned by

relative year, whereas climate–growth correlations used the available calendar-year overlap between each group-position chronology and the climate record (Section 2.6).

$$\text{Year} = Y_0 - (N - n), \quad (1)$$

For living trees (SL and LL), $Y_0 = 2022$. For the ten standing dead trees (DT), Y_0 was 2017 for tree 5039; 2018 for trees 3317, 3442, 3507, 4721, 4850, 5021, and 5031; and 2019 for trees 3315 and 3468. This procedure established the exact calendar-year correspondence for each cross-section.

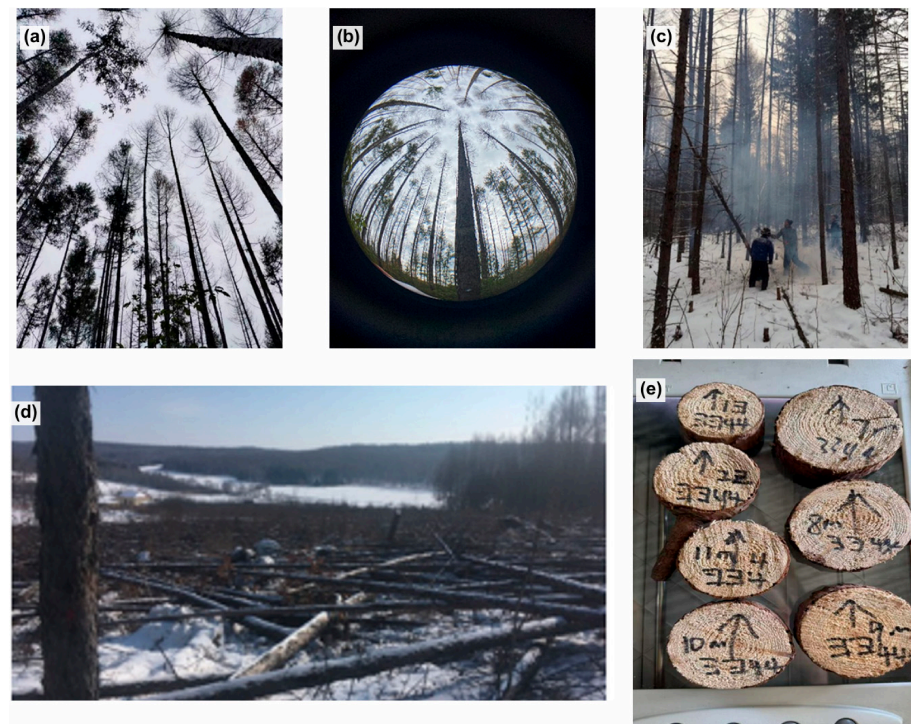


Figure 1. Field survey, sample-tree felling, and stem-disc samples from the *Larix olgensis* plantation. (a,b) Stand conditions before felling; (c) tree survey and felling in the study stand; (d) stand conditions after felling; and (e) stem discs collected and labelled at different stem heights.

2.5. Growth Metrics and Relative-Height Standardisation

To compare longitudinal growth among trees of different heights, actual sampling heights were converted to relative stem height. After excluding the stem tip, non-standard sections, and anomalous sections, the sampling height of the highest valid disc for each tree was used as the reference for standardisation. For each tree, discs nearest to 0%, 25%, 50%, and 75% relative stem height were selected for longitudinal comparisons, with 0% representing the stem base. The disc at breast height (1.3 m) was included separately as a fixed absolute-height position for comparison with growth at relative stem heights. The diameter characteristics of the three tree groups at these five stem positions are summarised in Table 2.

Tree-ring width (TRW) was used to characterise local radial growth at different stem positions. To compare recent growth using a standardised 15-ring window, the outermost 15 consecutive rings were extracted for each tree and sampling position. Rings within this window were renumbered from relative year 0 to 14, where 0 denotes the earliest ring and 14 denotes the outermost ring. Mean recent TRW for each tree and sampling position was calculated as the average of these 15 rings and was used to compare recent growth levels among SL, LL, and DT. To express recent radial growth as annual cross-sectional area growth, we additionally converted TRW to basal-area increment (BAI) for the directly

sampled discs nearest 0%, 25%, 50%, and 75% relative stem height. Annual BAI was calculated as $BAI_i = \pi (R_i^2 - R_{i-1}^2)$, where R_i and R_{i-1} are the cross-sectional radii at the end and beginning of year i , respectively [37]. Mean recent BAI was calculated over the same outermost 15-ring window. Descriptive statistics for mean recent BAI among the three tree groups at the four relative stem heights are presented in Table 3.

Table 2. Diameter characteristics of the three tree groups at five stem positions.

Tree Type	Group Name	Stem Position	Mean Diameter $\pm$ SD (cm)	95% CI (cm)
Small living trees	SL	0%	11.86 ± 2.12	11.05–12.67
		1.3 m	10.91 ± 1.45	10.36–11.46
		25%	8.32 ± 1.61	7.71–8.94
		50%	7.40 ± 1.45	6.85–7.95
		75%	5.63 ± 1.27	5.14–6.11
Large living trees	LL	0%	18.96 ± 2.96	17.71–20.21
		1.3 m	18.14 ± 2.44	17.11–19.17
		25%	13.24 ± 2.06	12.37–14.11
		50%	11.57 ± 1.98	10.74–12.40
		75%	8.85 ± 1.90	8.05–9.65
Standing dead trees	DT	0%	12.07 ± 1.78	10.80–13.34
		1.3 m	10.76 ± 1.61	9.61–11.91
		25%	8.37 ± 1.39	7.37–9.36
		50%	7.15 ± 1.69	5.95–8.36
		75%	5.78 ± 1.88	4.43–7.12

Note: Values are means $\pm$ SD; CI denotes the 95% confidence interval of the mean.

Table 3. Mean recent basal-area increment (BAI) among tree groups at four relative stem positions.

Tree Group	Relative Stem Position	n	Mean BAI $\pm$ SD (cm ² year ^{−1})	95% CI (cm ² year ^{−1})
SL	0%	29	3.97 ± 1.57^b	3.37–4.56
SL	25%	29	2.34 ± 0.99^b	1.96–2.71
SL	50%	29	2.27 ± 0.90^b	1.93–2.62
SL	75%	18	2.00 ± 0.79^b	1.61–2.39
LL	0%	24	10.78 ± 4.14^a	9.03–12.52
LL	25%	24	5.26 ± 1.80^a	4.49–6.02
LL	50%	24	5.16 ± 1.91^a	4.35–5.96
LL	75%	19	4.21 ± 1.33^a	3.57–4.85
DT	0%	10	4.22 ± 0.90^b	3.58–4.86
DT	25%	10	2.49 ± 0.68^b	2.00–2.97
DT	50%	8	2.31 ± 0.55^b	1.84–2.77
DT	75%	6	1.87 ± 0.99^b	0.83–2.91

Note: Different letters indicate significant differences among tree groups at the same stem position (Holm-adjusted $p < 0.05$). CI denotes the 95% confidence interval of the mean.

Recent radial-growth trends were quantified by simple linear regression of TRW against relative year for the 15-ring series at each sampling position of each tree. The regression slope was used as the recent TRW trend metric (mm year^{−1}). Negative and positive slopes indicate declining and increasing TRW, respectively, within the recent-growth window.

Annual volume increment (AVI) was calculated to represent whole-tree annual volume growth. Interannual AVI dynamics were expressed as annual means of valid trees in each group from 1990 to 2022. To characterise recent AVI trajectories, linear and quadratic regressions were fitted to the AVI series of each tree from 2005 to the last valid year. The series ended in 2022 for living trees and in the year of death for dead trees, and only

trees with at least eight annual AVI observations were retained. This criterion retained all 63 trees in the final analytical dataset, comprising 29 SL, 24 LL, and 10 DT. Model support was compared using the corrected Akaike information criterion (AICc), with the quadratic model considered better supported when its AICc was at least 2 units lower than that of the linear model. Quadratic regressions were also fitted to annual group means for visualisation. For between-group comparisons, the slope of the individual-tree linear regression represented the mean net AVI change over the complete analysis interval. AVI was reconstructed from tree-ring series of stem discs by calculating annual basal-area increments for individual stem sections and summing them along the stem [38,39]. For each section, annual ring widths were accumulated from the pith outward to obtain the cross-sectional radius at the end of year i , and the annual basal-area increment ΔA_i was calculated as:

$$\Delta A_i = \pi(R_i^2 - R_{i-1}^2) \quad (2)$$

The annual basal-area increments of all sections were multiplied by their respective section lengths and summed to obtain AVI for each tree in year i :

$$AVI_i = \sum_j^n \Delta A_{i,j} \times L_j \quad (3)$$

where $\Delta A_{i,j}$ is the basal-area increment in year i for stem section j , L_j is the length of the corresponding stem section, and n is the number of valid sections included for a tree. The spacing between adjacent discs was 1 m. Ring widths were converted from mm to cm before calculation, and AVI is reported in $\text{cm}^3 \text{ year}^{-1}$.

2.6. Statistical Analyses

Individual trees served as the statistical units. We calculated group means and standard errors for graphical presentation. We analysed mean recent TRW and recent TRW slopes using separate linear mixed-effects models. Each model included tree group (SL, LL, and DT), stem position (breast height, 0%, 25%, 50%, and 75%), and their interaction as fixed effects, with tree identity included as a random intercept to account for repeated observations from the same tree. We analysed mean recent BAI using the same model structure at 0%, 25%, 50%, and 75% relative stem height. Holm-adjusted pairwise contrasts compared tree groups within each stem position. Within DT, we tested positional variation in mean recent TRW using a separate mixed-effects model, followed by Holm-adjusted contrasts of each relative stem position against breast height.

One-way ANOVA followed by Tukey's HSD test compared individual-tree mean net AVI changes among SL, LL, and DT because this analysis contained one value per tree. We report partial eta-squared for mixed-effects-model F tests and eta-squared for the AVI ANOVA. Table 4 summarises the principal model tests and analysis-specific numbers of trees and observations. Statistical significance was set at $p < 0.05$. To evaluate sensitivity to the limited DT sample, we refitted all principal growth models ten times, omitting one DT tree in each iteration.

Climate responses were evaluated using seasonal-window Pearson correlations over the maximum overlapping period between each group-position TRW series and the climate records. For individual correlations, temporal autocorrelation in both series was accounted for using the modified Chelton effective sample size, with the autocorrelation functions truncated at $\lfloor N/5 \rfloor$ lags [40]. Two-sided p values were calculated using $N_{\text{eff}} - 2$ degrees of freedom and used to describe position-specific associations.

To evaluate the coherence of temperature responses across stem positions, we conducted an additional group-level global test. For each tree group, the 25 correlations comprising five temperature indices and five stem positions were Fisher- z transformed and

averaged. The null distribution was generated from 20,000 common-phase randomised climate surrogates, preserving the temporal autocorrelation of each climate series and covariance among the climate variables [41,42]. Two-sided global p values were calculated from the surrogate distributions and adjusted across SL, LL, and DT using the Benjamini–Hochberg procedure. Statistical analyses were conducted using R version 4.5.2 (R Foundation for Statistical Computing, Vienna, Austria) and Python version 3.12.13 (Python Software Foundation, Wilmington, DE, USA), with the nlme package (version 3.1-168) used for mixed-effects models and SciPy (version 1.16.1) used for correlation analyses.

Table 4. Summary of principal statistical analyses of recent growth and annual volume increment.

Response	Effect	Trees/Obs.	df	F	p	Effect Size
Mean recent TRW	Tree group	63/292	2, 60	16.44	<0.001	0.354
Mean recent TRW	Stem position	63/292	4, 217	73.67	<0.001	0.576
Mean recent TRW	Group $\times$ position	63/292	8, 217	8.41	<0.001	0.237
Recent TRW slope	Tree group	63/292	2, 60	13.73	<0.001	0.314
Recent TRW slope	Stem position	63/292	4, 217	49.46	<0.001	0.477
Recent TRW slope	Group $\times$ position	63/292	8, 217	2.45	0.015	0.083
Mean recent BAI	Tree group	63/230	2, 60	40.42	<0.001	0.574
Mean recent BAI	Stem position	63/230	3, 158	111.49	<0.001	0.679
Mean recent BAI	Group $\times$ position	63/230	6, 158	26.63	<0.001	0.503
DT mean recent TRW	Stem position	10/44	4, 30	3.96	0.011	0.346
Mean net AVI change	Tree group	63/63	2, 60	22.42	<0.001	0.428

Note: Trees/obs. denotes the number of trees/tree-position observations. Effect size is partial η^2 for mixed-effects-model tests and η^2 for the AVI ANOVA.

3. Results

3.1. Growth Patterns in Relation to Tree Size and Survival Status

At breast height, LL had greater mean recent TRW than SL, whereas DT did not differ from either group (Figure 2a). Mean recent TRW showed a group $\times$ stem position interaction ($F = 8.41$, $df = (8, 217)$, $p < 0.001$, partial $\eta^2 = 0.237$; Table 4). LL had greater mean TRW than SL at all five sampling positions and exceeded DT at 0% and 75% relative stem height. None of the DT–SL contrasts were significant (Figure 2). Mean recent BAI showed the same main separation: LL exceeded both SL and DT at all four relative stem heights, whereas SL and DT did not differ (Tables 3 and 4).

Within DT, mean recent TRW varied among stem positions ($F = 3.96$, $df = (4, 30)$, $p = 0.011$, partial $\eta^2 = 0.346$). Mean TRW at 75% relative stem height was higher than at breast height (difference = 0.584 mm, 95% CI = 0.260–0.908 mm, Holm-adjusted $p = 0.004$), whereas the contrasts at 0%, 25%, and 50% were not significant (Figure 2f). The upper stem therefore showed the clearest longitudinal departure from breast-height growth in DT.

3.2. Temporal Growth Variation Among SL, LL, and DT

The TRW series of all three tree groups showed interannual variation and declining trends to different degrees within the recent-growth window (Figure 3). At breast height, LL maintained higher TRW in most years, whereas SL and DT had lower growth levels and DT approached SL during the later years (Figure 3a). At 0% and 25% relative stem height, LL also generally maintained higher TRW, while the DT and SL trajectories largely overlapped (Figure 3b,c). At 50% and 75%, differences among the three series remained evident, with substantial overlap between DT and SL near the outermost rings (Figure 3d,e).

Recent TRW slopes showed a group $\times$ stem position interaction ($F = 2.45$, $df = (8, 217)$, $p = 0.015$, partial $\eta^2 = 0.083$; Figure 4; Table 4). LL slopes were less negative than SL at all five positions and less negative than DT from breast height to 50% relative stem height.

DT slopes were more negative than SL at 0% and 25% in the full model, although these contrasts remained significant in seven and eight of the ten leave-one-DT-out iterations, respectively. Their estimated directions remained unchanged across all iterations.

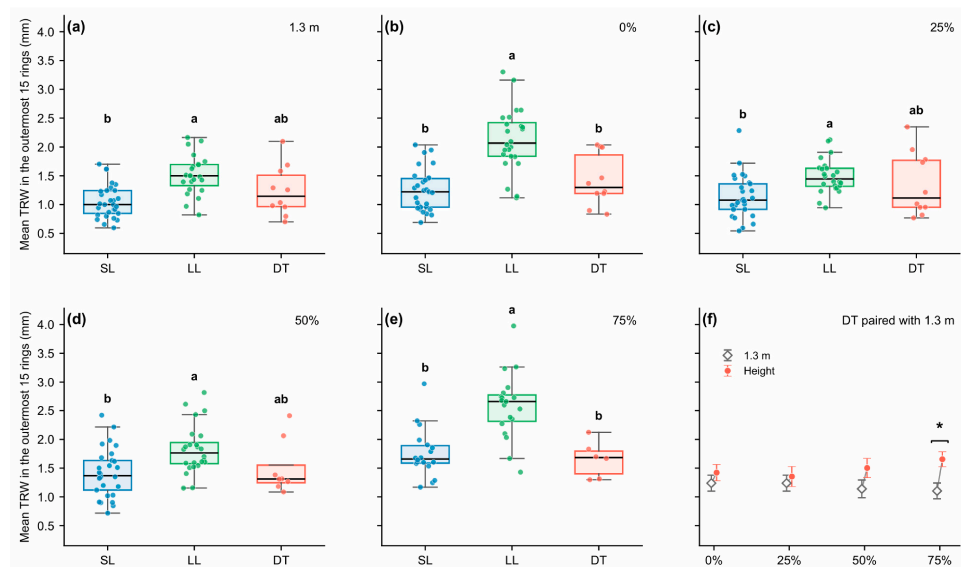


Figure 2. Distribution of mean recent TRW at breast height and different relative stem heights. Panels (a–e) show individual-tree mean TRW at breast height (1.3 m) and at 0%, 25%, 50%, and 75% relative stem height, respectively. Centre lines and box boundaries indicate medians and interquartile ranges, respectively, and points represent individual trees. Different lowercase letters indicate significant Holm-adjusted between-group contrasts from the linear mixed-effects model ($p < 0.05$). (f) Paired mean TRW of DT at each relative stem height and at breast height within the same tree; points and error bars represent means and standard errors, respectively. An asterisk indicates a significant Holm-adjusted contrast with breast height ($p < 0.05$).

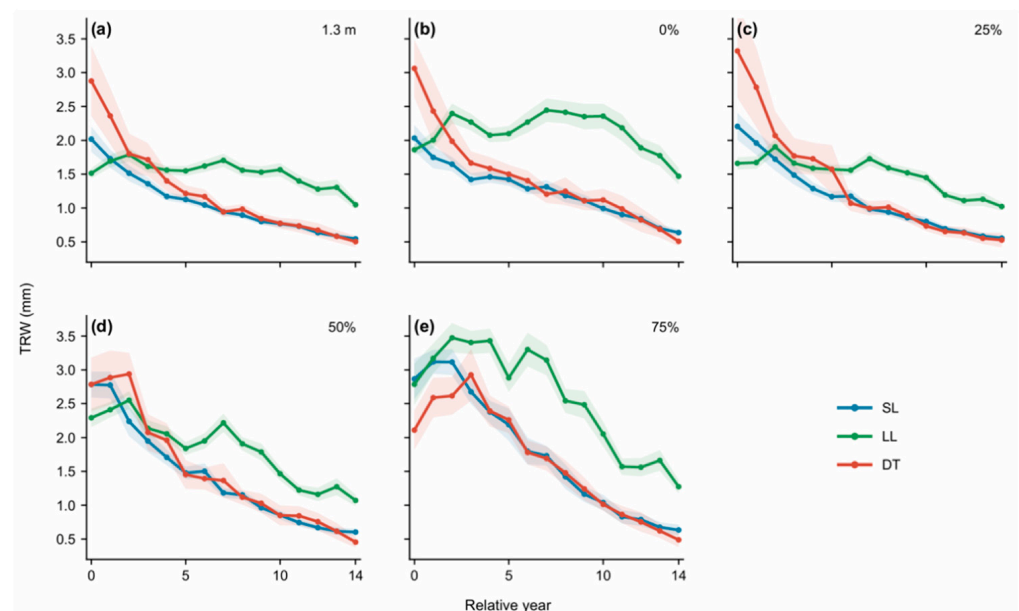


Figure 3. Recent TRW trajectories at breast height and different relative stem heights. Panels (a–e) show TRW time series at breast height (1.3 m) and at 0%, 25%, 50%, and 75% relative stem height, respectively. The x-axis shows relative year, with larger values closer to the outermost ring. Lines and shaded areas represent means and standard errors, respectively.

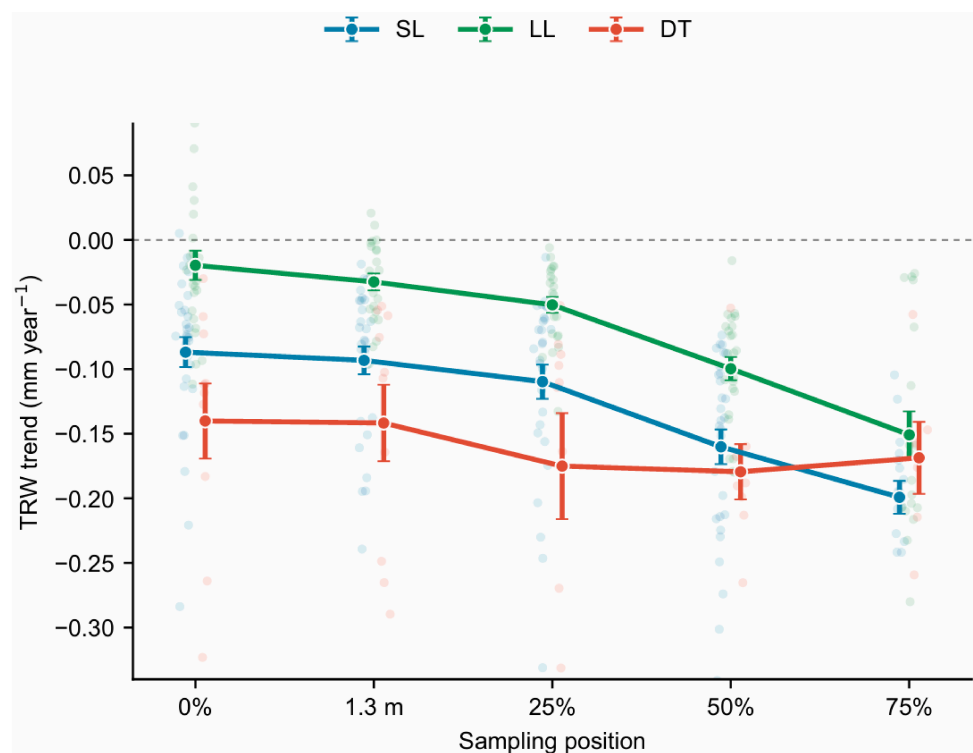


Figure 4. Recent TRW trends at different stem positions. The x-axis shows sampling positions at 0% relative stem height, breast height (1.3 m), and 25%, 50%, and 75% relative stem height. The y-axis shows the linear trend of TRW against relative year for individual trees. Faint points represent individual trees; lines and error bars represent means and standard errors, respectively. The horizontal dashed line indicates a trend of zero.

3.3. Dynamics of Annual Volume Increment

AVI dynamics differed among SL, LL, and DT (Figure 5). LL maintained greater AVI than SL and DT throughout the observation period, whereas the lower SL and DT trajectories overlapped in most years. Quadratic models received stronger AICc support than linear models for 48 of the 63 individual-tree series. Quadratic fits to the annual group mean indicated AVI peaks around 2008, 2012, and 2016 for DT, SL, and LL, respectively, followed by subsequent declines (Figure 5a). Across the complete interval from 2005 to the last valid year, individual-tree mean net AVI change differed among the three groups ($F = 22.42$, $df = (2, 60)$, $p < 0.001$, $\eta^2 = 0.428$; Table 4). Mean net AVI change was positive in LL ($176.99 \text{ cm}^3 \text{ year}^{-2}$) and negative in SL and DT (-45.26 and $-131.29 \text{ cm}^3 \text{ year}^{-2}$, respectively). LL was significantly higher than SL and DT, whereas SL and DT did not differ significantly (Figure 5b).

3.4. Seasonal Climate Responses of TRW at Different Relative Stem Heights

The group-level test supported a coherent negative temperature response across stem positions in LL (Fisher-z-aggregated mean $r = -0.351$, $p = 0.015$, $q = 0.045$), whereas the corresponding group-level responses were not significant in SL ($q = 0.696$) or DT ($q = 0.598$). At individual stem positions, six correlations had autocorrelation-adjusted $p < 0.05$ (Figure 6). Five occurred in LL: previous-growing-season mean temperature at 0% and 75% relative stem height, current-spring minimum temperature at 0% and 75%, and current-growing-season mean temperature at 25%. The remaining association occurred between current-spring minimum temperature and DT TRW at 75% relative stem height.

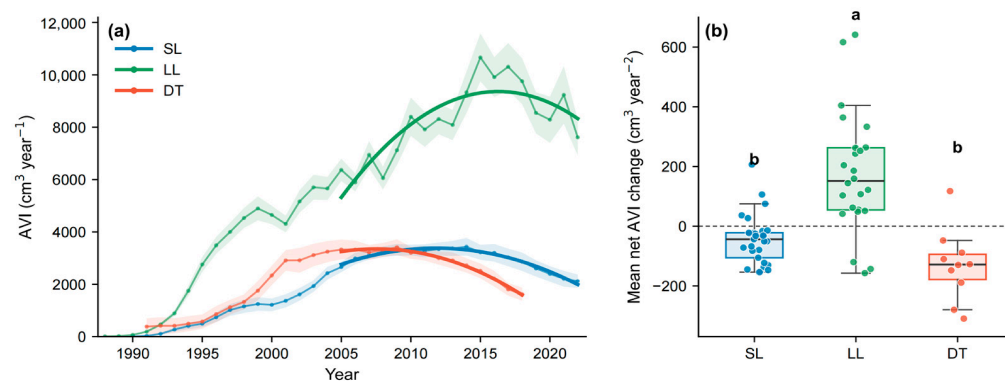


Figure 5. AVI dynamics and mean net changes among SL, LL, and DT. (a) Interannual variation in annual volume increment (AVI). Points connected by thin lines and shaded areas represent annual means and standard errors, respectively; thick curves show quadratic fits from 2005 to the last available year for each group. (b) Mean net AVI change for individual trees from 2005 to the last valid year, estimated as the linear slope over the complete interval. Centre lines and box boundaries indicate medians and interquartile ranges, respectively, and points represent individual trees. Different lowercase letters indicate significant between-group differences according to Tukey's HSD test ($p < 0.05$).

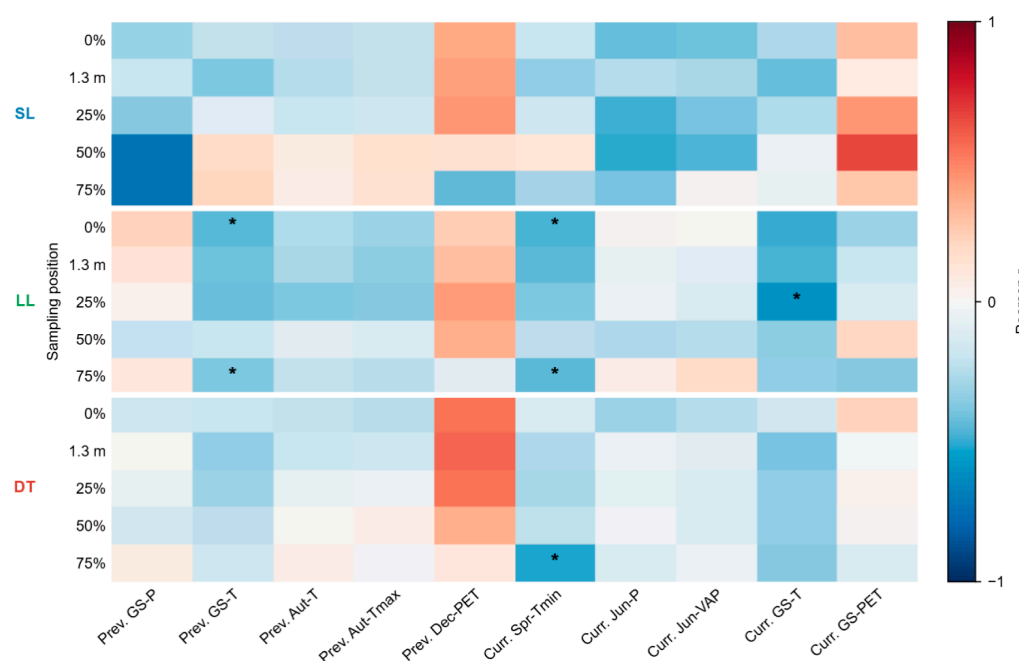


Figure 6. Seasonal climate responses of TRW among SL, LL, and DT at breast height and different relative stem heights. Colours indicate Pearson correlation coefficients between TRW and seasonal climate variables, with red and blue indicating positive and negative correlations, respectively. Asterisks indicate $p < 0.05$ after effective-sample-size adjustment for temporal autocorrelation. Prev. and Curr. denote the previous and current year, respectively; GS, Aut, Spr, Jun and Dec denote the growing season, autumn, spring, June and December, respectively; and P, T, Tmax, Tmin, PET, and VAP denote precipitation, mean temperature, maximum temperature, minimum temperature, potential evapotranspiration, and vapour pressure, respectively.

4. Discussion

4.1. Longitudinal Stem-Growth Patterns in Relation to Tree Size and Survival Status

The longitudinal growth profile of LL reflected both larger stem dimensions and sustained radial production. Because a given ring width produces a greater basal-area increment as stem radius increases [37–39], BAI and AVI capture size-related production

that cannot be evaluated from TRW alone. The higher TRW of LL across stem positions, together with its greater BAI and positive net AVI change, shows that its growth advantage involved continued whole-stem production as well as stem geometry. This interpretation agrees with Central European experiments showing that the relationship between tree size and growth varies with site conditions and resource availability [23].

Longitudinal growth allocation is shaped by crown proximity, hydraulic transport, and mechanical support. Radial increment can differ between the stem base and crown base [21], while mechanical exposure can promote basal allocation and stem taper [22]. These processes provide a physiological and structural context for the height-dependent growth profiles observed here. BAI did not resolve a consistent difference between SL and DT, whereas the timing of their AVI trajectories differed. Multi-height sampling therefore separated the longitudinal distribution of recent radial growth from longer-term whole-tree production. Long-term differences in stem size also integrate accumulated growth history. The LL profile therefore reflects sustained radial production as well as the geometric effect of a larger stem radius. Combining TRW, BAI, and AVI distinguishes local ring formation from its consequences for plantation productivity.

4.2. Growth Decline in Dead Trees Is Reflected in Both Radial and Volume Growth

Tree mortality results from multi-year declines in physiological function and accumulated environmental stress. Reduced carbon assimilation, impaired hydraulic transport, increased respiratory costs, and persistent climatic stress can reduce growth capacity and ultimately increase mortality risk [4,43–45]. Tree-ring studies have shown that radial growth often declines before tree death, although the duration and magnitude of decline depend on species, stand structure, competition, and climatic context [10,46,47].

DT combined coordinated recent decline across several stem positions with an earlier AVI downturn, indicating that pre-death growth weakening extended from local cambial activity to whole-tree volume production (Figures 3–5). AVI therefore complements position-specific TRW in reconstructing pre-mortality growth trajectories [38,39].

Most of this evidence, however, comes from breast-height chronologies [10,46,47]. By resolving growth decline along the stem and linking it to AVI, the present analysis extends this framework to whole-tree production. A plausible mechanism is the cumulative restriction of carbon assimilation and hydraulic transport: persistent stress can reduce cambial activity at multiple stem positions, while the resulting loss of cross-sectional growth is integrated into declining AVI [42–44]. The earlier AVI peak in DT therefore represents a shift from spatially distributed radial weakening to reduced whole-tree production.

SL represented a contrasting growth state, with recent weakening concentrated near the upper stem and a later AVI peak than DT. Because the upper stem lies close to crown carbon supply but remains hydraulically distant from the roots, its cambial activity can respond strongly to resource restriction [18,19]. The contrast between localised upper-stem weakening in SL and coordinated whole-tree decline in DT suggests that growth deterioration in an even-aged plantation can differ in spatial extent as well as magnitude.

4.3. Longitudinal Structure of Seasonal Temperature Sensitivity

The negative temperature response across LL stem positions is consistent with temperature effects on cambial activity, stem water dynamics, and xylem formation [48–50]. Its occurrence at multiple stem positions indicates that climate sensitivity extended beyond the conventional breast-height chronology [18,19].

In DT, the association with current-spring minimum temperature was concentrated at 75% stem height, where crown phenology, hydraulic transport, and cambial activity may exert stronger influence [18,19,28,50]. The distributed LL response and upper-stem

DT association indicate that multi-height sampling captures climate–growth variation not represented by breast-height series alone.

Previous studies of *L. olgensis* have mainly examined climate sensitivity across provenances, elevations, slope positions, and sites [26,29–32]. The present results add a within-tree dimension by showing that seasonal temperature sensitivity can be distributed along the stem. The coherent LL response may reflect the respiratory and transpirational demands associated with sustained growth, whereas the upper-stem DT association is consistent with close coupling among crown phenology, hydraulic transport, and cambial activity [18,19,28,50]. Multi-height analysis therefore complements regional dendroclimatic studies by resolving where climate sensitivity is expressed within a tree.

Regional climate data cannot fully represent within-site variation in soil moisture and microtopography, and multi-height stem analysis requires destructive sampling. The even-aged, single-species plantation reduced variation in tree age and species composition and therefore defines the primary scope of inference. The structurally and environmentally heterogeneous conditions of natural forests can produce different size–growth relationships and tree-to-stand scaling [23,24]. The group-level climate analysis identified coherent patterns, while individual climate sensitivity can vary among trees and over time [51]. The DT sample comprised ten trees from one plantation; validation across additional stands incorporating crown condition, competition, soil moisture, and continuous mortality records would clarify the generality and mechanisms of these patterns.

5. Conclusions

Growth differentiation among trees varying in size and survival status emerged both along the stem and at the whole-tree scale. LL combined greater TRW than SL across all sampling positions with greater BAI and whole-tree AVI than both SL and DT. DT showed coordinated recent TRW decline at multiple stem positions and an earlier AVI downturn, whereas BAI contrasts between DT and SL remained non-significant across relative heights. LL showed a coherent negative temperature response across stem positions, while the DT association was concentrated at 75% stem height. Together, these findings identify longitudinal stem variation as a key dimension linking tree size, survival status, growth capacity, whole-tree production, and climate sensitivity. Multi-height stem analysis therefore complements conventional breast-height chronologies in retrospective reconstructions by locating pre-mortality growth weakening and climate responses along the stem.

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