Radial growth anisotropy and temporality in fast-growing temperate conifers

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RESEARCH PAPER

Radial growth anisotropy and temporality in fast-growing temperate conifers

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Abstract

· *Key message* **Radial growth in a group of *Pinus radiata* D. Don. trees varies in magnitude around the circumference and follows synchronous but arrhythmic dynamics.**

· *Context* Eccentric and irregular girth growth is typically associated to specific growth responses, but it is generally assumed to be small or absent during normal development. The dynamics by which excess growth is formed are unclear.

· *Aims* The objective of this study is to determine if growth anisotropy is a commonly occurring phenomenon without apparent mechanical imbalance of the tree and to document the temporality of differential radial growth.

· *Methods* Six mature *P. radiata* trees were equipped with point dendrometers at different circumferential positions. Growth rates and periods of activity were monitored over 4 months.

· *Results* The highest growth differential on a single tree exceeded a factor of two. The direction of the highest growth varied between trees. In one case, that direction switched over time. The amount of anisotropy was explained by differences in the number of growing days and growth rate entropy.

· *Conclusion* Tree stem formation in fast-growing softwoods is a biological process characterized by high spatial heterogeneity and intermittent temporal activity.

Keywords Radial growth · Tree stems · Dendrometer · Anisotropy · Environmental forcing · Conifers

1 Introduction

Wood is a highly heterogeneous material. The degree of heterogeneity is a defining factor for the value and the performance of lignocellulosic materials that can be recovered from timber. Heterogeneity derives from the activity of the vascular

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cambium, a sheath of pluripotent cells responsible for wood formation in trees and shrubs. Cambial activity is known to be discontinuous in time and in space (Kozlowski and Pallardy 1996). New xylem cells are subject to internal and external controls that correspond to prevailing conditions at the time of formation. Once formed, the cells undergo programmed death, thus fixing them in a final state defining their geometry and physical characteristics. Variation in cambial activity is responsible for the spatial patterns of wood properties. As summarised by Larson (1969), 'wood quality is the result, wood formation is the process.' To understand how the spatial patterns arise, it is essential to know the history of growth velocity so that internal position can be linked back to the time it was formed. To that end, it is also important to determine if growth velocity itself varies spatially.

Radial growth can be anisotropic and display a direction-dependent magnitude. Differential growth activity around the circumference is typically associated to specific growth responses such as fluting (Julin et al. 1993), reaction wood (Timell 1986), or flexure wood (Telewski 1989) formation. Irregular cross-sectional shapes are common in coniferous tree stems. To the depressed stem regions correspond an increased

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rate of anticlinal divisions, possibly induced by local internal pressure in the cambial zone (Bannan 1957). More severe cases of circumferential variation can lead to the formation of discontinuous or fused growth rings (Larson 2012). Those may be found in less vigorous trees: senescing, heavily defoliated, or suppressed by competition (Kozlowski and Pallardy 1996). Knowledge is scarce about the potential occurrence of growth anisotropy in healthy trees under normal development. In addition, little is known about the dynamics of anisotropic growth when it occurs. It is often studied based on the ring structure of cross-sections, i.e. after losing the notion of time.

In temperate forests, trees exhibit growth periodicity associated to large-scale annual fluctuations in key environmental variables (daylength and temperature). Those fluctuations are the primary oscillations driving the intra-annual dynamics of radial growth. They are well documented and treated as normal development (Rossi et al. 2007; Cuny et al. 2014). The time variation of cumulated growth during the annual period generally follows a sigmoid function (Fritts 2012) but variation at shorter time scales may perturbate that main trend. Those secondary oscillations are typically episodes of reduced or interrupted radial growth. They may be observed during unfavourable environmental conditions such as drought-rain alternance (Larson 2012) or deficit in tree water storage (Zweifel et al. 2016), in relation to competition status (Drew and Downes 2018), phenology (Morel et al. 2015), or an internal redirection of resources during secondary flushes (Devine and Harrington 2009) or towards reproductive growth. Those sub-seasonal oscillations have been the subject of very few studies, but they indicate that cambial activity may be semi-discrete in time. It is also important to determine if those oscillations affect the cambial surface synchronously, as they would otherwise induce temporal dissociation in wood formation over the surface.

The measurement of spatial variability in radial growth dynamics introduces inevitable trade-offs. Measurement can be done well by attaching automated point dendrometers (Deslauriers et al. 2007; Drew and Downes 2009; De Swaef et al. 2015) at multiple positions on a tree stem (Zweifel et al. 2014). This method ensures a high time resolution although spatial resolution is limited to the number of sensors placed on the tree. It has been used in relation to wood quality (Bouriaud et al. 2005). The disadvantages of the method are that stem radial displacement (i) does not separate between alternate divisions towards phloem and xylem and (ii) does not capture the process of cell maturation (Cuny et al. 2015). Automated band dendrometers are unsuitable to describe the circumferential variation of growth as the measure of girth averages out any local growth differential in radial displacement. Pinning has been evaluated as a precise method to describe seasonal dynamics of wood formation (Mäkinen et al. 2008). Like the micro-coring technique, it can separate xylem from phloem

growth increments. However, both methods do involve destructive sampling. The chronology of wood formation is built using samples collected at different positions on the cambial surface as a substitute for time, which is an approach confounding temporal effects with those due to shifting positions. An excellent alternative to multiple point dendrometers is laser scanning of stem surface. This non-contact method can provide detailed spatial maps of cambial kinetics (Dünisch and Rühmann 2006). The disadvantages of laser measurement are very specialized equipment, deployment in field conditions, and long-term monitoring.

The main research question addressed in this study is whether radial growth can be anisotropic during the seemingly normal development of mature forest conifers in a temperate climate. We test a key associate hypothesis that growth anisotropy does proceed, at least partly, from asynchronous growth dynamics. We also test if short-term (days to weeks) fluctuations of growth activity are present, and possibly coherent, in non-limiting environmental conditions.

2 Material and methods

2.1 Plant material and study site

Six *Pinus radiata* trees with distinct genotypes were studied. They were planted in 2001 in a clonal archive near the Scion nursery in Rotorua, North Island, NZ (176.269 long., − 38.156 lat., 300 m a.s.l.). Initial stocking was equal to 1000 stems ha^{-1}. They were selected after visual assessment for straightness and lack of severe fluting. They covered a broad range of diameter at breast height (20–55 cm, see Table 1). Soil at the study site is documented as loam over sandy loam, deep (> 1 m), and well drained, with high permeability (> 72 mm h^{-1}) and high available water capacity (AWC > 160 mm for 0–100 cm layer) in the national S-map database (smap.landcareresearch.co.nz/, Lilburne et al. (2012)). Annual rainfall (July 2017–June 2018) was 1638 mm and mean annual temperature was 12.2 °C (MetService Rotorua airport station).

2.2 Monitoring of stem radial displacement

Dendrometers were mounted at breast height in three different configurations. Three trees, referred to as P1, P2, and P3, had a proximal sensor configuration. On each tree, two dendrometers were positioned 10 cm apart tangentially on either side of the north direction (referred to as NE and NW). Two trees, O1 and O2, were set with a pair of dendrometers, each on an opposite side of the stem, one facing north (N) and the other facing south (S). The last tree, labelled Q, was set up in a quadrant configuration with four dendrometers (Sellier and Ségura 2020). Each of them was oriented along a cardinal direction. The metal frames on which

Table 1 Tree diameter and growth characteristics. *DBH* is the initial diameter at breast height; *growth rate* is the radial growth rate averaged over directions; *anisotropy* is defined here as the ratio of maximum growth rate to minimum growth rate between directions; *concurrency* refers to the amount of time where growth was active or inactive in all directions at once—it is given as a fraction of the monitoring period. The complement to concurrency (e.g. for tree O1, 100−71.7 = 28.3%) represents the time fraction when growth was active in (at least) one direction but inactive in another

Tree	DBH (cm)	Growth rate (mm/year)	Anisotropy	Concurrency (%)
Q	50.4	7.9	1.75	63.8
O1	32.5	7.9	2.13	71.7
O2	56.4	9.1	1.38	74.8
P1	38.5	8.8	1.45	79.5
P2	20.9	2.3	1.52	67.7
P3	36	6.5	1.07	87.4

sensors were mounted have been fixed to the tree at a slight angle from vertical to minimize the disruption of sap flow at the point of measurement.

Two types of point dendrometers were used in this study. Linear variable differential transformers (Bestech, Australia) and linear variable potentiometers (LM10, Radiospares, UK) have been inter-calibrated before the experiment using a custom-built 3D-printed scale. The design of the scale permitted to convert raw millivolt signal to a physical displacement along the travel of the dendrometer. To avoid any problem of linearity, we kept a security margin of 10% at both extreme positions of the point of dendrometer. In that case, both technologies presented a linear electrical response, respectively (1.2152–1.3393 mm/V) for LVDT and (0.4732–0.4864 mm/V) for LM10. Sensor output was scanned every 30 s by two dataloggers (CR800, Campbell Scientific, USA) equipped with multiplexors and the 5-min mean value was recorded. The experiment lasted from December 22, 2017, to April 28, 2018.

2.3 Environmental data

Environmental data was collected by a weather station (CR3000, Campbell Scientific, USA) in an open site 200 m away from the studied trees. High-quality research-grade sensors recorded the following variables: air temperature (°C, 2 m above ground level), relative humidity (%), soil water potential (SWP, kPa, at 10, 20, and 30 cm depth), photosynthetically active radiation (PAR, MJ m^{-2}), rainfall (mm), and wind speed (m s^{-1}). All variables were recorded every 15 min except soil potential every 1 h. Vapour pressure deficit (VPD) was calculated from air temperature and relative humidity using the Tetens equation.

2.4 Data processing and analysis

Time series of stem radial displacement were processed for analysis. The processing steps consisted of (i) converting voltage to radial displacement, (ii) resampling the series to a regular time interval, (iii) correcting for large jumps in displacement such as caused by re-positioning or a voltage drop, (iv) compensating for the thermal expansion of both sensor and mounting frame (1 μm/°C), and (v) offsetting the series so that the initial displacement is zero. Signal processing was done using Python version 3.7 (Python Software Foundation, http://www.python.org) and the pandas library (McKinney 2010). After processing, stem radial displacement was split into growth (GRO) and stem water deficit (SWD). The value of GRO at any time is the maximum of either current displacement value or previous GRO value. The definition is based on the Zero Growth concept (Zweifel et al. 2016). Daily increments were calculated as the successive differences of GRO at midnight. The SWD component was calculated by subtracting the GRO component from stem radial displacement series. Daily SWD values are the daily maximum. Two generalized additive mixed models (GAMM) were used to evaluate environmental forcing of GRO and SWD, respectively. Fixed effects were represented by the daily mean of each environmental variable except air temperature (daily minimum). Tree and direction were treated as random effects. The GAMM analysis was done using R 3. 6.1 (R Core Team 2019) and the mgcv package (Wood and Wood 2015).

Growth anisotropy between two circumferential positions was defined by the ratio of total growth between the position with greater growth to that with lower growth. A linear model of anisotropy was created using R 4.0.0 and selected as the model with the lowest Akaike Information Criterion. Five potential predictors were considered:

- The distance between sensors.
- The relative difference of activity between locations, where activity is the number of days when the growth rate is not zero.
- The relative difference in vigour, where vigour is the total growth achieved over the number of growing days.

- Concurrency is a simple measure of synchrony. It is defined as the fraction of the monitoring period during which the growth rate is zero or non-zero for all sensors on a stem at once.
- Cross-sample entropy (Richman and Moorman 2000) is an elaborate measure of asynchrony. It characterizes the degree of coupling and complexity between two time series. Entropy was calculated with a custom R function for a 2-day scale and a 7-day scale. Because of the collinearity between both, only the 2-day scale results were used.
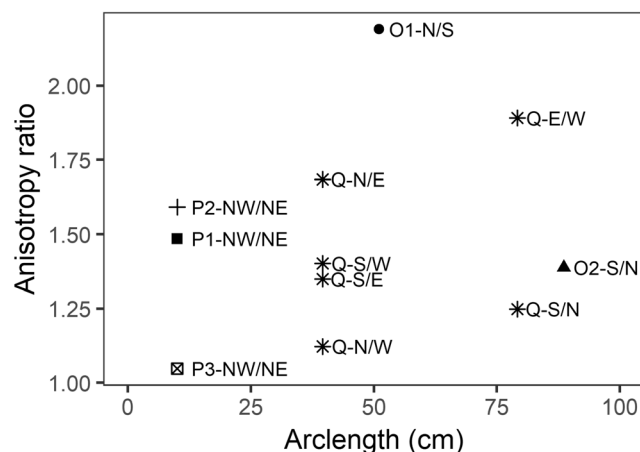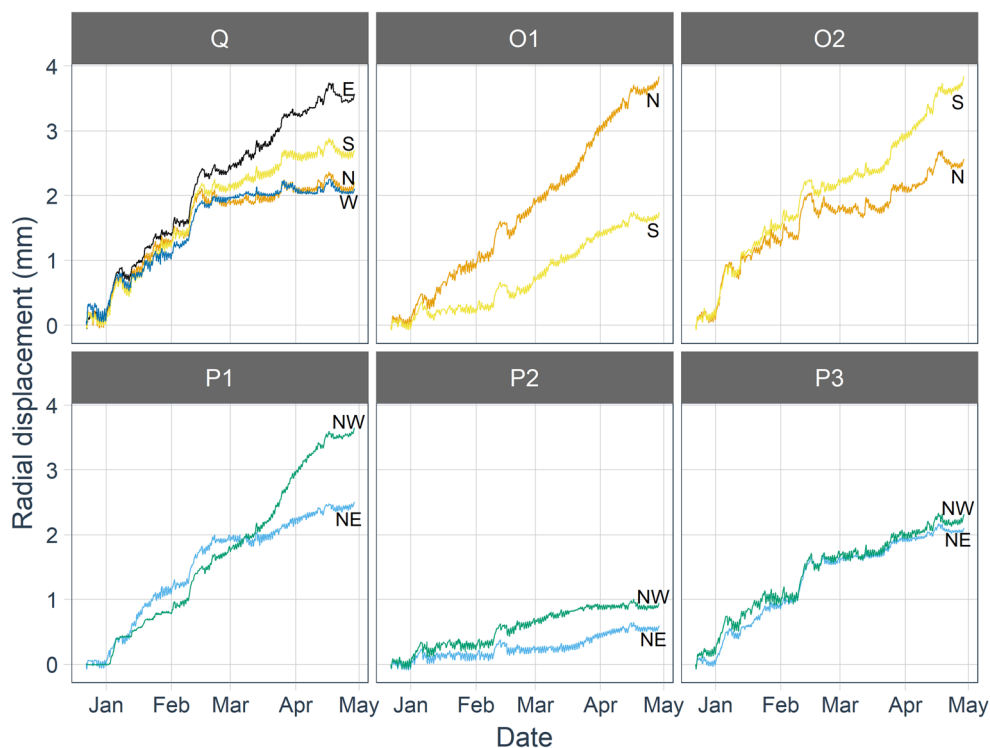
The relative importance of predictors was evaluated using the relaimpo package and the lmg method (Grömping 2006).

3 Results

3.1 Radial growth anisotropy

Figure 1 shows the stem radial displacement of the six studied trees. All trees but tree P3 displayed a favoured growth direction. Four sensors on four different stems measured a growth increment greater than 3.5 mm, equivalent to a 10 mm year^{-1} mean radial growth rate. The main growth direction varied among the trees: north for tree O1, south for tree O2, east for tree Q, and north-northwest for tree P1. Importantly, the favoured direction in the case of tree P1 switched at the end of summer. The north-northeast orientation was initially favoured for two-thirds of the monitored period. It indicates

Fig. 2 Growth anisotropy as a function of distance between circumferential positions. Anisotropy is defined as the ratio of maximum-to-minimum growth increments for two given directions on a tree stem. Positions are labelled by tree and directions

that excess growth in one direction is a time-dependent feature and not only a local amplification of growth magnitude. Similarly, the radial increment measured for the sensor Q-E started to exceed that of other directions from mid-February onwards. For many sensors that measured a lower growth increment (c. 2 mm), the growth loss was apparently caused by a slow down after mid-February. As an exception to this trend, little growth was measured on O1-S until mid-February and became pronounced afterwards. In that case, the initial delay was responsible for the relative lack of growth on the south side of the stem.
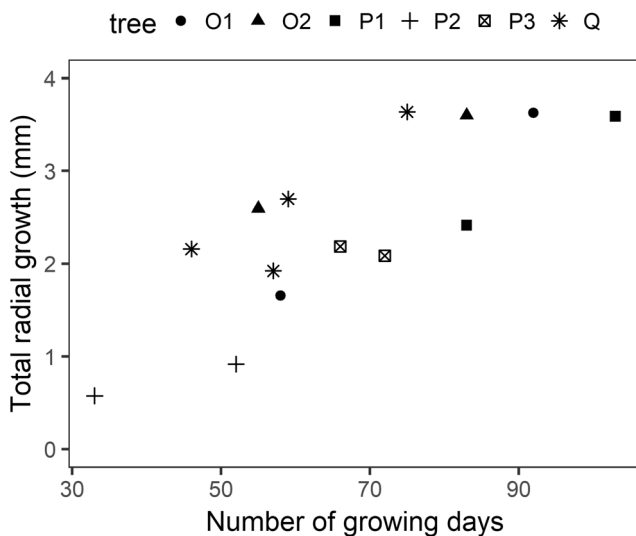
Fig. 1 Stem radial displacement at breast height as a function of tree and sensor position. Each subplot corresponds to a different tree stem. Stem positions are labelled for cardinal directions: N, North; S, South; E, East; and W, West

Fig. 3 Radial growth magnitude as a function of activity. Growing days are defined as days with a non-zero daily growth rate

The radial growth ratio between two different points on the same tree stem is above 1.25 at the majority (8 out of 11) of position pairs that were monitored (Fig. 2). While the highest recorded ratios were measured in sensor pairs placed on opposite sides of the stem (O1-N/S and Q-E/W), there is no clear relationship between the anisotropic ratio and the circumferential distance between sensors (Fig. 2). Remarkably, some of the sensors positioned 10 cm apart in a similar direction (P1-NW/NE and P2-NW/NE) presented a large growth differential despite the proximity. This indicates that anisotropy occurs over small spatial scales too.

Growth activity was extremely variable between and within trees: it ranged from 26 to 81% of the entire monitoring period. Only half the sensors recorded growth for more than half the period. As a trend, radial growth increased with the number of growing days, but deviation from the trend could be pronounced (Fig. 3). For instance, the growth increment for Q-N, equal to 3.6 mm, was produced in 75 days while similar radial growth took 28 more days to produce at P1-NW. Tree stem positions that displayed moderate growth levels also showed a broad-ranging activity. In the case of Q-N, it took almost twice as many growing days as P1-NE (83 vs. 46) to produce a similar amount of growth (2.16 vs. 2.41). This led us to define the active growth rate (in relation to the number of growing days instead of total) to represent the vigour of radial growth at a stem location. There is also a general trend of total growth increasing with vigour with large deviations from the trend, either with moderately vigorous positions achieving high growth (e.g. O1-N) or with vigorous positions achieving average growth levels (e.g. Q-N).

It was found that the degree of growth anisotropy between two circumferential locations was best predicted using the relative difference in activity between those positions, and the cross-sample entropy of the daily growth rate time series in a linear model ($F = 9.9$ on 2 and 8 degrees of freedom, $p = 0.007$, adjusted $r^2 = 0.64$). The relative contribution of each predictor was similar: 52.5% for activity and 47.5% for entropy. Other characteristics of the growth responses such as the relative difference in vigour, the circumferential distance separating the sensors, and asynchrony were poor predictors of anisotropy.

3.2 Sub-seasonal growth rhythms

The daily growth rates measured at all positions exhibited a strong variability (Fig. 4). The standard deviation represented from 0.99 to 2.29 times the mean growth rate depending on the position. A key aspect was that growth occurred by sequences of activity followed by episodes of no measured growth. Those episodes lasted up to a month in the worst case. There were phases when nearly all monitored positions grew at once: early January, mid-February, late March, and mid-April. There were also phases when no growth was recorded at all positions, e.g. late December or late April. Both phase types are referred to as group growth and group deficit, respectively. Between those phases, radial growth was measured only for a fraction of the locations and not necessarily the same ones. It is referred to as individual growth as it appeared specific to each location. The frequent interruption of growth caused adjacent radial position to be formed at different times, up to a month (Fig. 5). Conversely, large amounts of seasonal growth (up to 1 mm) could be produced in a week's time.

Radial growth dynamics were well correlated within and between trees (Fig. 6). The best correlation was always obtained without delay, which indicates growth activity was synchronous overall. This must be nuanced by the fact that concurrency for each tree ranged from 60 to 87%. For up to a third of the monitored period, one stem position grew while another did not. Whereas correlation between two growth rate series was generally higher between different positions of a given tree, it could also be higher across trees (e.g. $r = 0.92$ for P1-NE and Q-E) than on the same tree ($r = 0.6$ for P1-NE and P1-NW).

Analysis of the time series of growth rate in the frequency domain revealed no main rhythm in growth activity (Fig. 7). No frequency peak was observed in the power spectra. However, the spectra showed a marked inflection at a characteristic period of 3–4 days. The amount of growth increased rapidly for periods up to 3 days. It kept increasing with period length for longer periods longer but more slowly. This is likely caused by the occurrence of growth interruptions during those longer periods. The successive differences in daily growth rate, excluding phases of inactivity, followed a random normal distribution (Fig. 9 in the Appendix). This further supports the absence of a coherent pattern in growth rate variability.

3.3 Environmental forcing

Figure 8 shows the daily growth rates and SWD at two positions on different trees. Both the growth and deficit signals have a distinct temporal signature on each tree. The position O1-S showed a lot of activity for the second half of the monitoring period whereas that episode was absent at position Q-N. The situation was reversed for the first half of the monitoring period, with active growth recorded for Q-N while very little activity was noted for O1-S. We refer to periods of activity like these as periods of individual growth as they appear specific to the position of observation. Despite differences, both positions also grew concurrently at other times, along with nearly all other positions. We refer to those as windows of group growth. Group growth was typically associated with rain events (Fig. 8) although not all rain events induced group growth. It also occurred when VPD was very low (< 0.1 kPa). Group deficit was slightly more common than group growth. It also followed rain events when soil water potential dropped well below water holding capacity. It also co-occurred with drops in daily minimum temperature.

The correlation between growth rate and environmental variables were weak overall (Fig. 5). Most growth signals were significantly ($p < 0.01$) and negatively correlated with VPD and PAR without a lag. Growth occurred preferentially on humid, low-radiation days. When growth was not correlated with VPD, it was correlated with soil water potential (SWP) instead. Environmental variables explained 43.6% of the deviance in the GAMM of growth rate (adjusted $r^2 = 0.42$; see Table 2 in the Appendix).

4 Discussion

4.1 Radial growth varies circumferentially

In this study, the circumferential variation of radial growth was large. The growth rate differential measured on the different trees ranged from 7 to 113%. The observed anisotropy could be explained by the formation of compression wood (CW), which increases growth on the compressed side of a leaning tree (Wilson and Archer 1977; Timell 1986) and decreases it on the opposite side (Pallardy 2008). Although none of the studied trees showed any lean, CW formation cannot be ruled out. CW can also form in vertical tree stems (Telewski 2006) to generate growth stresses to correct an imbalance in mechanical loading induced, for example, by an asymmetrical distribution of crown weight (Archer 2013). The studied trees were in a stand that was thinned. It created small canopy gaps and a heterogeneous light environment that could lead to asymmetrical crown development and a CW response. It is the most likely explanation for the observed growth anisotropy. A response driven by the local light regime would be consistent with the direction of anisotropy varying between individuals. The dominant wind can also induce CW

Fig. 4 Daily radial growth rate as a function of tree and direction. Each subplot corresponds to a single tree stem. The cardinal directions are N, North; S, South; E, East; and W, West
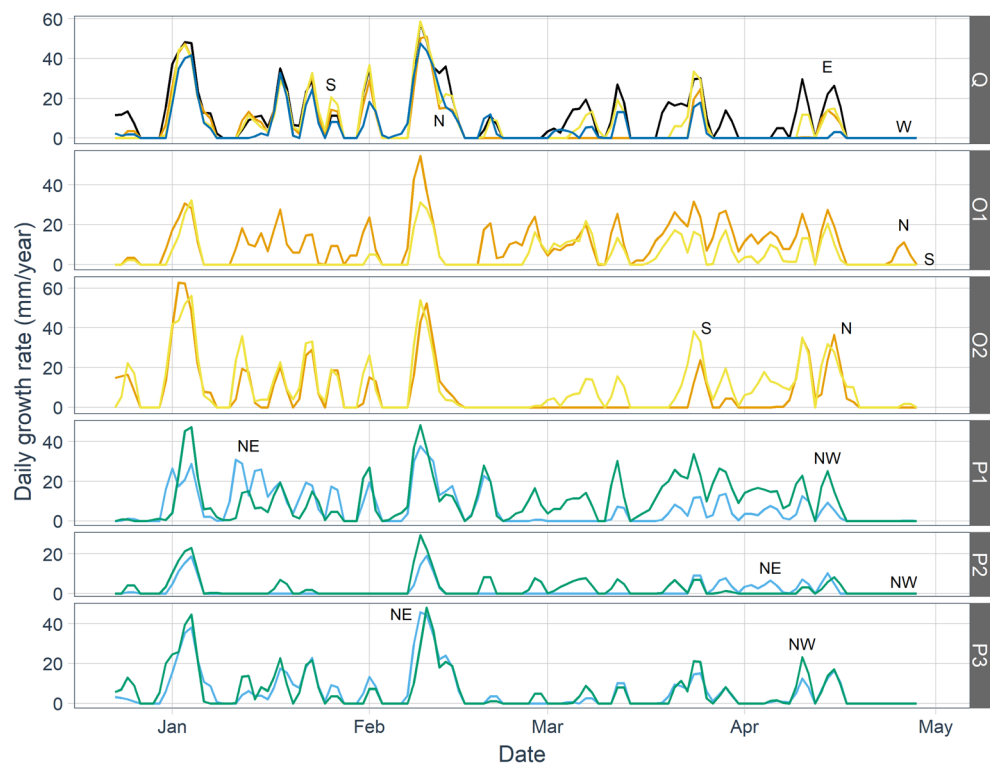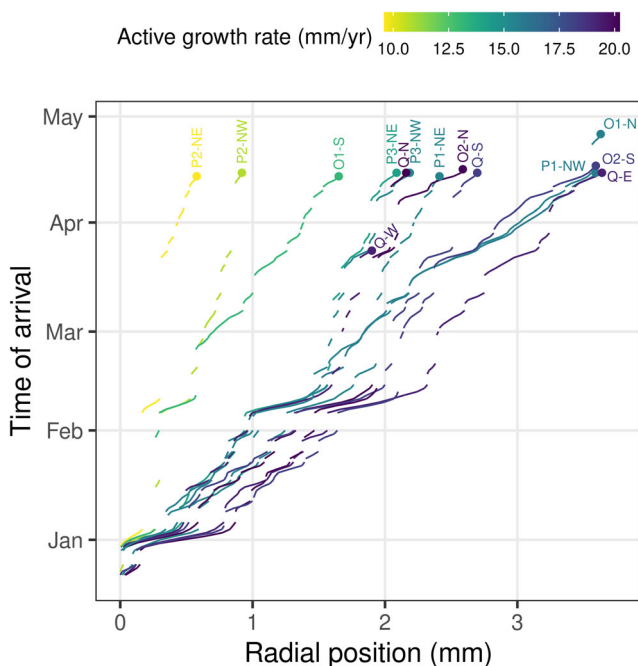
(Robertson 1990) but is unlikely to be the causative factor in this study. Otherwise, CW and eccentric growth would occur in the same direction for all trees, that of the dominant wind, and that was not the case. Without histological analysis, it is not possible to assert whether CW formed.
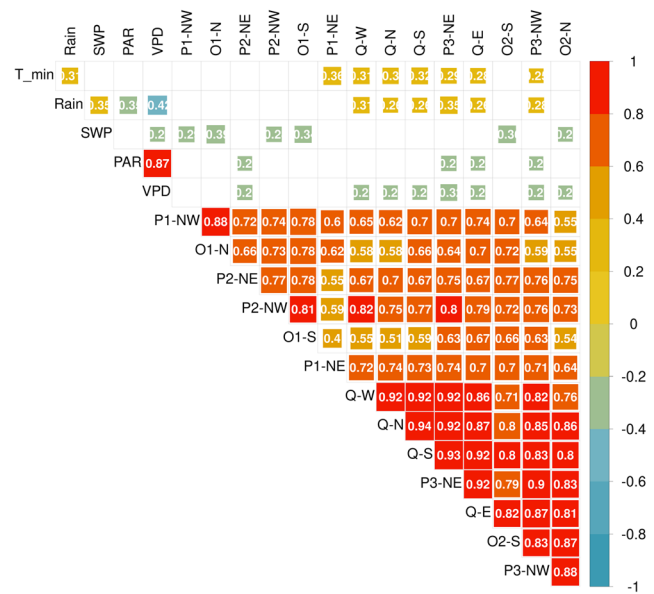
Although the underlying cause of anisotropy has not been identified, it was found to be associated with specific temporal features. The difference of growth duration combined with the lack of similarity in the temporal sequences of growth activity was found to be characteristic traits defining the growth differentials between two positions on a stem. Neither aspect alone was sufficient as both factors contributed equally. On the other hand, anisotropy was not explained by more vigorous growth at one location at the expense of another, nor by physical separation between positions as was expected. This highlights further the need to monitor the development of anisotropy in real time as opposed to analysing the final shape of growth rings.

4.2 Radial growth is synchronous (most of the time)

Excess growth did not originate from completely different dynamics. Growth activity was found to be generally synchronous for all stem positions. The time series of daily growth rate were well correlated both between trees and within a tree. The best correlation was always observed without lag. Growth synchronization has been reported both at multiple heights in a single tree (Bouriaud et al. 2005; Zweifel et al. 2014) and in different trees (van der Maaten et al. 2013). The latter study

Fig. 6 Correlation matrix of daily radial growth rate and environmental variable time series. Sensors are labelled by tree and direction. Environmental variables are minimum daily air temperature (T_min), rainfall, soil water potential at 30 cm depth (SWP), photosynthetically active radiation (PAR), and vapour pressure deficit (VPD). Values given at a row-column junction corresponds to the maximum Pearson correlation coefficient between the row variable and the column variable. Non-significant correlations ($p > 0.01$) are not shown

refers to synchronization with meteorological drivers, however, and emphasizes the significance of inter-tree variability of growth. The difference of radial growth dynamics between individuals can also be significant between size classes (Wunder et al. 2013).

Although present, synchronization was partial. At tree level, a position was actively growing while another position was
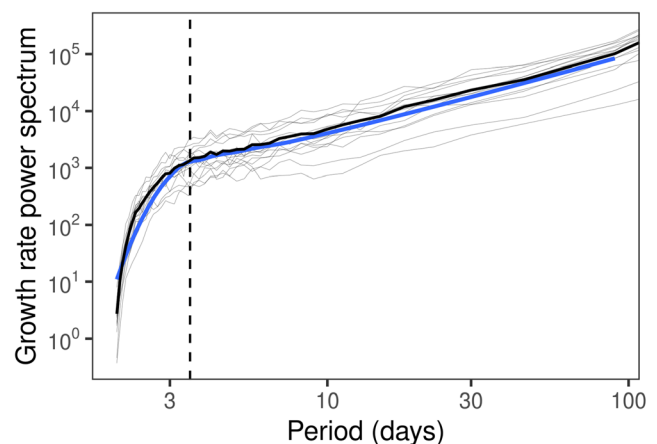

Fig. 5 Time of arrival of outer bark at a given radial position. The colour bar indicates the mean active growth rate (growth amount divided by growing days) of each position

Fig. 7 Power spectrum of daily growth rate time series (arbitrary units). Thin black lines correspond to individual sensors. The thick black line corresponds to the mean spectrum. The blue line is a smoothed trend (loess smoothing) for indicative purpose. The dashed line ($t = 3.5$ days) marks spectrum's inflection

not growing typically 25% of the time. In that respect, each position had distinct segments of activity. Those segments occurred in-between several key periods where nearly all stem positions grew or stopped growing together. In summary, any growth response appeared to share both coherent sequences and sequences with an individual signature. The coherent sequences were instrumental to anchor all growth signals on the time axis and to synchronize them. Synchronicity does not imply that the cambium reactivates or enters dormancy at similar times on different trees. Onset and cessation of cambial

activity vary with species and tree size and status (Rathgeber et al. 2011; Michelot et al. 2012). Yet, it seems that from the moment the cambium is active, it is subject to global influences captured by all individuals.

4.3 Environmental forcing (and its limits)

Radial growth is a process known for being under strong environmental control (Gruber et al. 2009; Köcher et al. 2012). Automatic dendrometers are a key in investigating

Fig. 8 Time variation of radial growth rate, selected environmental variables, and stem water deficit (SWD). Growth rate and SWD are given for stem positions O1-S and Q-N. The blue-green areas indicate days when more than 90% of all measured stem positions (n = 14) were growing. The brown areas indicate days when less than 10% of all stem positions were growing. Group growth and group deficit label some time regions when 90% of all stem positions are also in the same state, growing or in deficit, respectively. Individual growth labels give an example of region when the corresponding stem position is behaving differently from the other one. The environmental variables shown are daily rainfall photosynthetically active radiation (PAR), soil water potential (SWP) at 30 cm depth, and vapour pressure deficit (D)
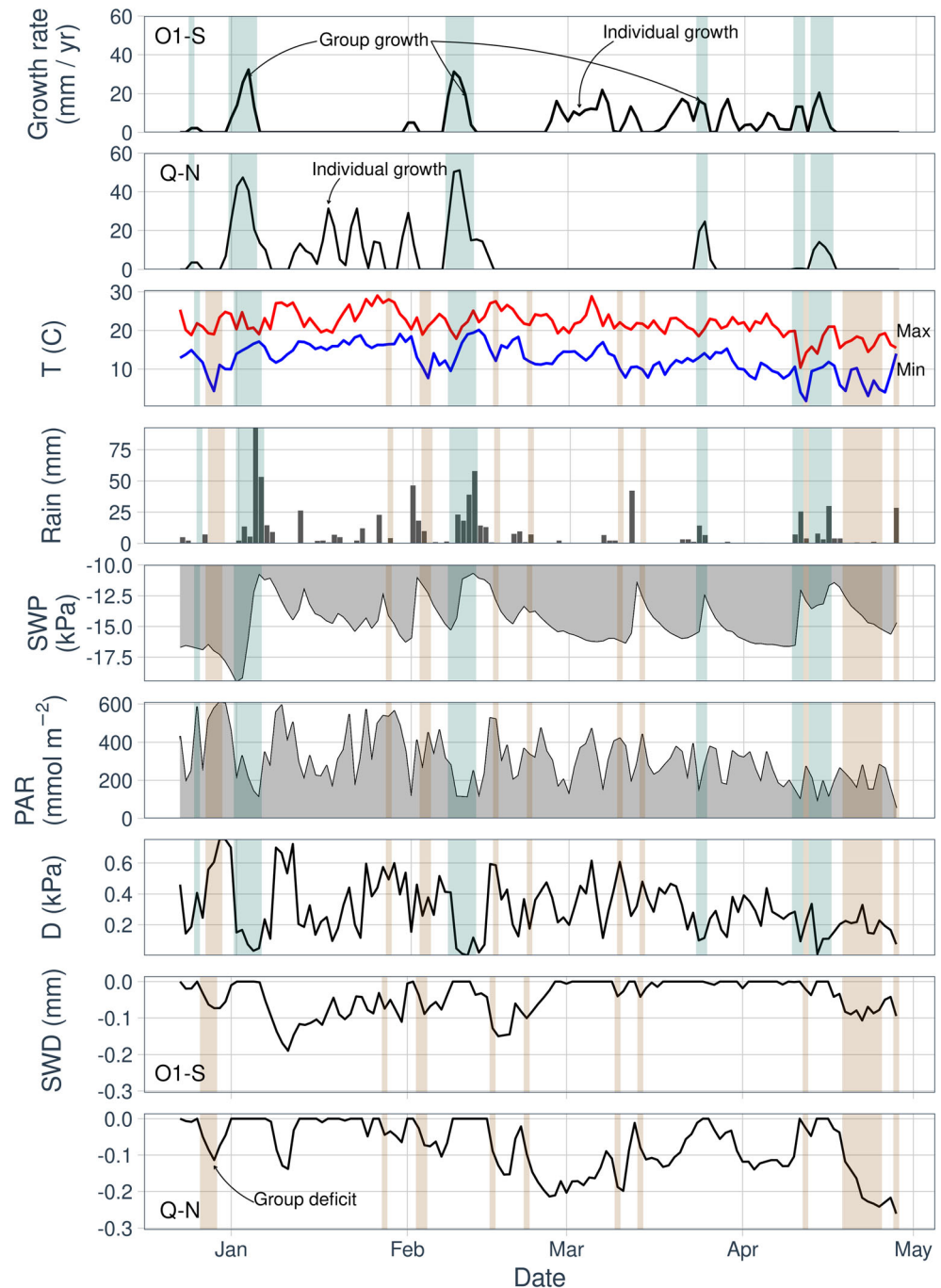
short-term growth responses to the environment (Drew and Downes 2009) and, in general, tree-environment interactions (Cocozza et al. 2018). Several meteorological and soil variables drive important physiological processes. Solar radiation limits the amount of sugars photosynthesized by leaves. Those are critical for osmotic regulation and cell wall formation. Both soil and atmospheric water (SWP and VPD) impact xylem's water potential, stomatal conductance, cell turgor, and growth. Temperature plays an important role in biochemical processes and reaction rates (Gillooly et al. 2001). It has a measurable effect on cellular processes such as mitosis (Vaganov et al. 2006). Disentangling the respective influences of environmental factors can be difficult as they interact with each other. Despite that difficulty, the physical environment is the prime candidate for inducing a shared response in a group of trees (van der Maaten et al. 2013).

In this study, air temperature affected growth rates in only half the stem positions. Only the minimum daily temperature was important, which is consistent with growth mostly occurring at night. Water availability also affected growth either via rainfall (Trees Q and P3) or soil water potential (Trees O1 and O2). Both aspects should be linked, as SWP would increase after a rain event. The relative sensitivities of each tree could be due to their genotype. Growth and VPD were also often correlated but weakly. The GAMM analysis also showed a nonlinear relationship between growth and VPD. High VPD levels would reduce growth because of the elevated evapotranspirative demand. In isohydric species such as *P. radiata*, excessive transpiration induces stomatal closure (Rodríguez-Gamir et al. 2019), which interrupts the absorption of carbon dioxide. It can restrict growth directly by limiting the levels of assimilates used for manufacturing structural carbohydrates in the developing cell wall. It can also restrict radial growth by failing to maintain the osmotic potential and turgor in enlarging xylem cells. Because PAR is well correlated to VPD, we observed the counter-intuitive situation where growth was higher on days of low ambient light. A negative relationship between PAR and stem radius variation has been reported but attributed to changes of stem water content rather than growth (van der Maaten et al. 2013). In this study, PAR was associated to growth. However, the association was not widespread. It was only significant for a few stem positions. It is also worth noting that PAR exceeded saturating light levels only on 17 days at mid-day. Even in non-saturating conditions, PAR was the least growth-limiting of all environmental factors. It may be related to the particularities of the photosynthetic system of *P. radiata*.

4.4 Arrhythmicity

Approximately half the stem positions were subjected to a long (2 weeks or longer) deficit period in addition to the typical intermittent response described above. A long deficit period with markedly low SWD values is associated with a depletion of stem water storage and a decrease in soil water potential (Zweifel et al. 2001). It is unclear why long-term deficit occurred at some stem positions and not at others, sometimes on the same tree. Difference between trees could be explained by differences of genotype, micro-climate, soil variability, and tree social status. However, those aspects do not explain the variation in SWD responses within a single tree. Intra-tree variation must relate to a heterogeneous distribution of water and growth substances around the circumference. A highly uneven distribution of cohesive water in stem cross-sections has been documented (Westhoff et al. 2009). Local variation in water (and carbohydrates) would affect osmotic potential and water potential in and around the bark tissues. It could explain why some regions are under stress while other are not. It would also explain local differences in cambial activity. The uneven supply of water and carbohydrates must proceed from sectorial transport of those substances. The very limited amount of transport in the tangential direction has been shown separately for both xylem and phloem using dyes (Kozlowski et al. 1967; Larson et al. 1994) and isotope tracers (Orians et al. 2004; Kagawa et al. 2005; De Schepper et al. 2013).

Another confounding aspect of long-term deficit is that it occurred at different times. Some positions entered long-term deficit early in the monitored period, then recovered and returned to baseline activity. Other positions first followed baseline activity but exhibited long-term deficit at a later stage. It is difficult to reconcile that a stem position can be susceptible to water stress and have partially depleted water reserves on any month yet remain relatively well hydrated the next month despite similar rain/soil water conditions. Those changes of sensitivity to stress over time could be linked to the seasonal allocation patterns and the dynamic reconfiguration of phloem connections (Kagawa et al. 2005). It could also result from changing conditions at either end of the hydraulic pathways (foliage and fine roots) propagating down to the connected stem region. Those aspects are still poorly characterized.

We observed that growth operated as a semi-discrete process repeatedly interrupted by short-term periods of inactivity. Some of those episodes were associated with night-time residual stem shrinkage, which is a common marker of water stress (Zweifel et al. 2001; Zweifel et al. 2016). It appears as if those mild water stress events interrupted the main rhythm of radial growth. This intermittent behaviour was present on all trees in any direction. However, soil water potential, soil available water capacity, the frequency, and amount of precipitation were all representative of a mesic environment. There is no indication of drought conditions during the summer the study took place. It is likely that many episodes with slightly negative SWD values were

only lack of growth; those episodes were caused by a set of conditions temporarily unconducive to xylem cell production or expansion. Only the rare phases with markedly negative SWD values were possibly indicating an actual depletion of stem water reserves. Altogether, it seems that trees growing in a mild temperate climate such as the North Island of New Zealand are not subject to a single environmental constraint, thus making it difficult to parse the nature of environmental control. Alternately, it is possible that for fast-growing temperate forests, as for tropical forests, the role of endogenous control in growth periodicity (Alvim 1964) becomes prevalent.

5 Conclusion

In five out of six trees, the growth differential around the circumference was not negligible and could exceed a factor of two. The variation was pronounced even over short distances. Circumferential variation was not limited to magnitude. It also affected dynamics or, perhaps, growth dynamics were responsible for anisotropy. A larger number of trees each equipped with more sensors will be essential to assess the extent of anisotropy taking place during wood formation. It will be invaluable to quantify the amount of intra-tree variability compared to inter-tree variability, a better-known aspect. Despite the direct role of environmental influences on cambial growth regulation, future studies would benefit to focus on characterizing physiological variables and internal transport processes to elucidate the causative factors of anisotropy and growth temporality.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix
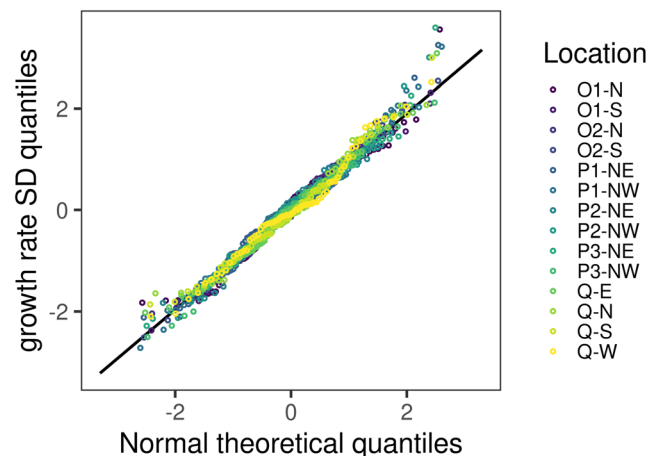
Fig. 9 Quantile distribution of the successive differences (SD) in daily radial growth rate by dendrometer. A SD value is the growth rate difference between two successive days. Inactive periods (two successive zero growth days) were excluded. SD quantiles are given relatively to quantiles of a normal distribution

Table 2 Estimates for the daily growth rates over all the stem positions ($n = 14$) given by the GAMM model using smoothed environmental variables as fixed effects. Approximate significance code: '***': $p < 0.001$. Effective df: effective degree of freedom

Approximate significance of smooth terms	Effective df	F
$s(T_{min})$	7.52	9.17***
$s(Rain)$	8.18	14.31***
$s(SWP)$	7.74	62.08***
$s(VPD)$	8.3	27.28***
$s(PAR)$	3.41	5.7***
	Value	
Observations	1764	
r^2 (adj.)	0.421	
Deviance explained	43.6%	

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