Temperature and water potential co-limit stem cambial activity along a steep elevational gradient

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1. Abstract

- Efforts to develop mechanistic tree growth models are hindered by the uncertainty on whether and when tree growth responses to environmental factors are driven by carbon assimilation or by biophysical limitations on the wood formation.

- In this study, we use multiannual weekly wood-formation monitoring of two conifer species (Larix decidua and Picea abies) along a 900 m elevational gradient in the Swiss Alps to assess the biophysical effect of temperature and water potential on wood formation. To this end we developed a model that simulates the effect of water potential on turgor-driven cambial division, modulated by the effect of temperature on enzymatic activity.

- The model reproduced the observed phenology of tracheid production, as well as intra- and inter-annual tracheid production dynamics of both species along the elevational gradient, although inter-annual model performance was lower. We found that temperature alone explains the onset of tracheid production, yet water potential appears necessary to predict the ending and the total amount of tracheids produced annually.

- We conclude that intra-annual cambial activity is strongly constrained by both temperature and water potential at all elevations, independently of carbon assimilation. At the inter-annual scale, biophysical constraints likely interact with other factors.

Keywords: Cambial activity; conifer; sink limitation; biophysical limitation; temperature; water potential; elevation gradient; treeline
Introduction

Forests are the main land carbon sink (Pan et al., 2011), but large uncertainties exist on the feedbacks between climate change and vegetation and on the future dynamics of this sink (Pugh et al., 2016; Keenan et al., 2016). Global warming is expected to promote vegetation growth in cold and humid environments and be deleterious in hot and dry environments (Klesse et al., 2018). Yet, heat waves and droughts have been shown to cause negative impacts on vegetation even in cold and humid areas (Allen et al., 2010, 2015; Babst et al., 2019), as temperature-related increases of atmospheric water demand may offset the beneficial effect of warming (Barber et al., 2000). At the same time and potentially owing to climate change-induced drought, the direct fertilization effect resulting from increasing atmospheric [CO$_2$] might be more limited than expected (Peñuelas et al., 2011; Silva & Anand, 2012; Van Der Sleen et al., 2015).

Vegetation models, including Dynamic Global Vegetation Models (DGVM), are critical tools to simulate vegetation-atmosphere interactions at a global scale. Current DGVMs forecast increased land carbon uptake in the future (Anav et al., 2013; Sitch et al., 2013; de Almeida Castanho et al., 2016) but these projections are uncertain as models struggle to reproduce vegetation response to climate and [CO$_2$] variability (Babst et al., 2013; Smith et al., 2016; Klesse et al., 2018). Potential explanations for these discrepancies include model misrepresentation of carbon allocation rules (De Kauwe et al., 2014), population demographics (Bugmann & Bigler, 2011), nutrient cycling (Wärlind et al., 2014) and plant’s carbon source (i.e. carbon assimilation) and sink (i.e. cambial activity) interactions (Fatichi et al., 2014) (reviewed in Hickler et al., 2015; Pugh et al., 2016). Among these uncertainties, the sink limitation issue has received so far limited attention compared to the growing body of experimental evidences and its large modelling implications (Fatichi et al., 2019; Friend et al., 2019).

Although both carbon assimilation and cambial activity are directly controlled by temperature ($T$), water potential ($\psi$) and nutrients, cold and drought stress may limit cambial activity more than photosynthesis (Körner, 2015). Cell division in the cambium is strongly inhibited at $T$ and $\psi$ thresholds below which carbon assimilation is still substantial (Körner, 2008; Tardieu et al., 2015).
2011). As a consequence, tree growth is expected to be increasingly sink-limited under colder
or drier conditions, which is supported by the observation that carbohydrate storage tends to
increase towards high elevation tree lines (Hoch & Körner, 2012) or under drier conditions
(Körner, 2003; Sala & Hoch, 2009). Despite recent advances (e.g. Fatichi et al., 2014; Schiestl-
Aalto et al., 2015; Guillemot et al., 2017) the challenge of modelling sink limitations on tree
growth remains largely unmet. When compared to source-based modelling, adding sink
processes nevertheless yielded substantial differences in terms of model sensitivity to
environmental variables (Fatichi et al., 2014) and improved model predictions (Leuzinger et
al., 2013; Guillemot et al., 2017).

Monitoring xylogenesis provides qualitative and quantitative insights on the process of wood
tissue formation, which inform process-based modelling (Fritts et al., 1999; Vaganov et al.,
2006). The implementation of such principles within DGVMs has the potential to improve
predictions (Zuidema et al., 2018). During xylogenesis, cambial cells divide and differentiate
into tracheids through successive expansion, wall thickening, lignification and programmed cell
death (Rathgeber et al., 2016). Owing to the sequential nature of xylogenesis, wood volume
and mass increment are lagged in space and time (Cuny et al., 2015). Volume increment results
from cambial cell production and subsequent tracheid expansion, whereas most mass increment
is related to the fixation of cellulose and lignin during cell wall thickening and lignification,
which is also the process capturing the most carbohydrates. As a consequence, annual tree
volume (and diameter) increment is determined by the product of tracheid number and their
average dimensions at the end of the growing season, but is potentially decoupled from biomass
increment and carbon assimilation.

Because average cambial cell size is relatively stable during the growing season, cambial cell
volume must approximately double before dividing. Cambial cell division rate may thus be
related to the rate of cambial cell expansion (Vaganov et al., 2006). Plant cells expand when
cell turgor pressure overcomes a yield threshold, above which the expansion rate is linearly
related to turgor, as formalized by Lockhart (1965). Water potential ($\psi$) thus drives plant cell
expansion through its influence on turgor pressure, and strongly inhibits cambial activity below
c. –1 MPa (Hsiao, 1973; Muller et al., 2011; Cabon et al., 2020). Assuming that the whole stem
behaves like a single cell obeying to Lockhart’s equation allows to model sub-daily to seasonal
elastic and plastic stem diameter variations based on a detailed description of plant water relations (e.g. Génard et al., 2001; Steppe et al., 2006; Coussen et al., 2018). Coupling with an explicit representation of xylogenesis and sugar transport further permits deriving tracheid formation (Höltä et al., 2010). In spite of holding great promise, the complexity of this modelling approach currently holds back application to large temporal or spatial scales.

Wood formation models based on water relations typically lack an explicit formulation of $T$ effects. And yet, rates of tissue expansion, cell division and progression through the mitotic cycle have a highly consistent response to varying $T$ that can be modelled based on the effect of $T$ on metabolic activity (Parent et al., 2010; Parent & Tardieu, 2012). The active molecular bond breaking required for the cell walls to grow (Cosgrove, 2000) implies a dependence of turgor-driven cell expansion on $T$ (Nakamura et al., 2003). At chilling $T$ ($<10 \, ^\circ\text{C}$), the relation between cell division and metabolic activity may not hold, as mitosis is then inhibited (Inoué, 1964; Fuseler, 1975; Begum et al., 2012). Localized cooling or heating can thus trigger cambial dormancy or cambial reactivation (Oribe et al., 2001; Kudo et al., 2014; Begum et al., 2016).

The sensitivity of cambial activity to chilling $T$ is threshold prone, with threshold $T$ being estimated around 5 $^\circ\text{C}$ (Rossi et al., 2007; Körner, 2008). Considering that a certain time is needed in order to effectively observe tracheid differentiation, growth resumption in spring can thus be modelled based on above-threshold $T$ accumulation, while site- or species-specific variations might be related to chilling accumulation during the endo-dormant phase (Delpierre et al., 2018).

In this study we present a mechanistic model, conceptually anchored in the sink limitation framework (Fatichi et al., 2014, 2019), that integrates the biophysical effects of $T$ and $\psi$ on turgor-driven cell expansion to simulate the phenology and dynamics of intra- to inter-annual tracheid production ($P$). We apply this model to a unique dataset of multiannual weekly tracheid formation observations on two contrasting conifer species along a 1300–2200 m elevation transect in the Swiss Alps, up to the treeline. We specifically address the hypotheses that: (1) tracheid production phenology, as well as its intra- and inter-annual variation in both species along the elevation gradient can be explained by the effect of $T$ and $\psi$ on turgor-driven cell expansion, and that (2) $T$ and $\psi$ co-limit tracheid production all along the elevation gradient,
with $T$ limitations being dominant at higher altitudes and $\psi$ limitations becoming more important at lower elevations.
3. Material and methods

3.1 Tracheid production model

We introduce a mechanistic model that simulates daily radial softwood tracheid production (P), based on the biophysical limitations of water potential (ψ) and temperature (T) on cambial activity. We build on a previous study (Cabon et al., 2020) where Lockhart’s (1965) formalization of turgor-driven plant cell expansion was adapted to model the effect of ψ on cell enlargement during xylogenesis. Here we combine Lockhart’s equation (Eq. 3) with an equation describing the dependence of metabolic activity upon T (Johnson et al., 1942; Eq. 4) to simulate cell expansion and division in the cambial zone and the subsequent increment in the number of differentiating tracheids as a function of ψ and T.

Cell expansion rate (r) is defined as the relative time derivative of cell volume (V):

\[ r = \frac{dV}{Vdt} \]  

Eq. 1

Assuming that cell expansion is the process limiting cell division, that cambial cells divide every time they double in size and that each division instantly results in a cell exiting the cambium and initiating differentiation into a tracheid, tracheid Production Rate (PR) can be related to the cambial cell expansion rate such that (see details in Methods S1):

\[ PR = \frac{N_c}{\ln 2} \cdot r \]  

Eq. 2

where \( N_c \) is the number of cells in the cambial zone that is able to divide and is assumed to be constant (but see e.g. Cuny et al., 2013). Following Cabon et al., (2020), the dependence of cell enlargement on ψ during xylogenesis can be described using Lockhart’s (1965) equation for turgor-driven plant cell expansion:

\[ r = \phi (\psi - \gamma_{\psi}) \]  

Eq. 3

where \( \phi \) is the cell wall extensibility and \( \gamma_{\psi} \) is the water potential yield threshold and is equal to the sum of the osmotic potential (\( \pi \)) and the turgor yield threshold. Despite turgor pressure is the actual force driving cell expansion, we assume here that \( \pi \) is constant and thus that \( \psi \) is linearly related to turgor pressure and thus drives \( r \) (Fig. 1a). \( \phi \) is further assumed to be under
control (Nakamura et al., 2003) and is modelled using the equation proposed by Johnson et al. (1942), which has been used before to relate the dependence of plant growth rate upon $T$ (Parent et al., 2010; Parent & Tardieu, 2012) and represents the increase of chemical reaction rates with $T$ combined with the decrease of enzymatic activity due to reversible protein denaturation at high $T$:

$$\phi(T) = \phi_{\text{max}} \cdot \frac{T_K e^{\frac{\Delta H_A}{R T_K}}}{1 + e^{\frac{\Delta S_D}{R}(1 - \frac{\Delta H_D}{\Delta S_D T_K})}}$$  \hspace{1cm} \text{Eq. 4}

where $T_K$ is the temperature in Kelvin, $R$ is the ideal gas constant, $A$ is a scaling parameter, $\Delta H_A$ is the enthalpy of activation and $\Delta H_D$ and $\Delta S_D$ are the enthalpy and entropy difference between the catalytically active and inactive states of the enzymatic system. This function exponentially increases with low $T$, reaches its maximum at $T_{\text{opt}}$ and then drops as enzyme denaturation outweighs the increase in chemical reaction rates (Fig. 1b). Because these parameters were evidenced to vary little among species, $\Delta H_A$, $\Delta H_D$, and $\Delta S_D$ are derived from the literature (Parent et al., 2010; Parent & Tardieu, 2012) yielding $T_{\text{opt}} = 30 ^\circ C$, whereas $A$ is calculated such as $\phi(T_{\text{opt}}) = \phi_{\text{max}}$.

Finally, in order to account for the observations that xylogenesis only occurs when $T$ is superior to a given threshold ($\gamma_T$) (Rossi et al., 2007; Körner, 2008), it is assumed that cambial activity is paused (e.g. because of reversible microtubule depolymerization at chilling temperatures; Fuseler, 1975; Begum et al., 2012) and no division occurs when $T$ is below this threshold. PR is thus expressed as a function of $T$ and $\psi$, such as:

$$\text{PR}(\psi, T) = \begin{cases} \frac{N_c}{b n^2} \cdot \phi(T) \cdot (\psi - \gamma_\psi), & \psi > \gamma_\psi \cap T > \gamma_T \\ 0, & \psi \leq \gamma_\psi \cup T \leq \gamma_T \end{cases}$$  \hspace{1cm} \text{Eq. 5}

The parameters $\gamma_\psi$ and $\gamma_T$ are unknown and are estimated by calibration as detailed below. The full list of model symbols, abbreviations as well as the value of fixed parameters are given in Table 1.

### 3.2 Study area and tracheid production observations
We applied our model to a study area located within the Lötschental valley, in the central Swiss Alps (46°23'N 7°45'E). The valley is covered by mixed coniferous forests of larch (*Larix decidua* Mill.) and spruce (*Picea abies* (L.) Karst). Mean annual *T* is approximately 5 °C in the valley-bottom and 2.5 °C at the treeline. Mean annual precipitation exceeds 800 mm. Over the period 2009–2013, December was the wettest month and March the driest (Fig. S1). Seven plots were established (Fig. S2) along a transect including a 900 m elevation difference, from the valley bottom to the treeline, at four elevations (1300 m to 2200 m). Two plots were installed at each elevation on two facing slopes (NE and SW orientation), except at the valley bottom where only one plot was set up. Both spruce and larch are present at the five plots from the valley-bottom to 1900 m, whereas only larch is present at the highest elevation plots.

In order to gather observations of cambial phenology and intra-annual tracheid production, xylogenesis was monitored during 7 years at the valley-bottom and on the south slope (2007-2013) and 4 years on the North slope (2007-2010). At each plot, four mature and dominant trees per species were monitored each year (Table S1). The sampled trees were changed after the 2007, 2009 and 2011 growing seasons in order to reduce the impact of sampling-related wound reaction. The assessment of cambial activity was based on repeated cellular observations performed on micro-cores sampled weekly over the full growing season (April-November). Micro-cores collection and processing are described in Cuny *et al.* (2019).

Cumulative Production (CP) was measured on each microcore sample as the total number of cells outside the cambial zone. In order to separate intra-annual variability from the inter-individual and inter-annual variability, each yearly CP series was first standardized by its 95% quantile to obtain the relative Cumulative Production (CPr) and was then averaged at the plot and species level. For each sampling date, PR and PRr were derived from CP and CPr, respectively, as ∆CP/Δt and ∆CPr/Δt, respectively, where the difference is centered on the sampling date. In order to mitigate the methodological effect of circumferential variability (i.e. sampling on different points of the stem) on the data, the time-step Δt was set to one month. Shape constrained additive models (SCAM) were fitted to log-transformed CP using monotonically increasing smooth function with individual trees as a cofactor and assuming quasi-Poisson distribution of residuals (Pya & Wood, 2015).
Fitted SCAMs were used to interpolate the date of P onset, defined as the date of the first tracheid formation. On the other hand, as microcore sampling may yield misleadingly positive or decreasing CP once P has ceased (Rathgeber et al., 2018), nor CP nor PR can be used to estimate the cessation of P. The second derivative of CP was found to tend more consistently toward 0 at the end of the growing season, thus we defined the date of P cessation as the latest date where the second derivative of the fitted SCAMs was close to 0 (threshold=-0.001 day^{-2}; see Fig. S3 for comparison with tracheid enlargement phenology). Finally, the date of peak P was calculated as the date of overall maximum of the first derivative of the fitted SCAMs.

As the trees on which microcores were sampled varied depending on the sampling year, four trees (among the previously selected trees) per plot and species were additionally cored at the end of the 2015 growing season to estimate Annual Production (AP), with the objective to test model ability to reproduce interannual growth variations. Trees were cored on the sides facing and opposing the slope using an increment borer (Haglöf, Sweden). Digital images of the anatomical sections were used to identify tracheid position on the 2009-2013 rings with the image analysis software Image-Pro Plus (Media Cybernetics, USA), coupled with ROXAS (von Arx & Carrer, 2014). The radial number of tracheids in each ring was then estimated using the R package ‘RAPTOR’ (Peters et al., 2018). Standardized AP (APs) was calculated at the plot and species level by subtracting the mean and dividing by the standard deviation.

3.3 Model inputs: temperature and water potential

Air temperature (T_{air}) and soil moisture (SM) were both monitored on-site during the study period but measurements started in 2009 in the case of SM. Radiation-shield covered sensors were installed at each plot on a central tower (2.5 m above the ground) within the canopy to record T_{air} with a 15 min temporal resolution. Hourly SM was measured on two points and depths (10 cm and 70 cm) per plot using two/three sensors (Decagon, USA, EC-5) per point and depth. Soil texture and bulk density measurements at each plot and depth were used to estimate plot- and depth-specific parameters (Tóth et al., 2015) of van Genuchten’s water retention curves (van Genuchten, 1980). Soil water potential (\psi_{soil}) was then estimated from SM and averaged over depth. \psi_{soil} was also directly measured (Decagon, USA, MPS-2) during one year at the valley-bottom and South-facing plots (i.e. N13, S16, S19 and S22 in Table S1).
Measured $\psi_{soil}$ was then corrected for $T$ (Walthert & Schleppi, 2018) and used to validate $\psi_{soil}$ estimated from SM.

Twig water potential ($\psi_{twig}$) measurements were taken at two locations (at the valley bottom, and at the treeline on the South-facing slope, i.e. N13 and S22 in Table S1) during four diurnal campaigns (2-h interval from 05:00 to 21:00 CET on 19-04-2014, 27-05-2015, 21-07-2015 and 24-09-2015) and a weekly sampling at midday (11:00-15:00 CET) was performed during the 2015 growing season. Measurements were performed using a Scholander pressure chamber (Scholander et al., 1965) on four twigs (~5 cm) per tree. At the valley bottom and South-facing plots, stem hourly diameter variation were measured on two to four trees per plot and species from 2008 to 2013 using high-precision point dendrometers (Ecomatik model DR, Munich, Germany) mounted over bark at breast height on the side facing the slope (King et al., 2013a).

A Tree Water Deficit index (TWD) was calculated from dendrometer measurements as the difference between running maximum stem diameter and hourly stem diameter (Zweifel et al., 2001). These data were used to calibrate a linear regression between daily maximum relative TWD and measured midday $\psi_{twig}$, following Dietrich et al. (2018) ($R^2$=0.49; Fig. S4). Based on the simplistic assumption of a constant pressure difference between the crown and breast height, hourly trunk water potential ($\psi_{trunk}$) was then estimated from relative TWD by using the above-mentioned calibrated relationship minus the intercept (Fig. S5).

3.4 Model runs, calibration and validation

The P model (Eq. 7 and 8) was resolved using a finite time approximation at the daily scale. To fit the model time-step, sub-daily environmental variables were aggregated as follows. Because sub-daily soil $\psi$ variations are relatively small, $\psi_{soil}$ was aggregated to the daily scale by calculating the 24h-average (Fig. 3). In contrast, $T_{air}$ and $\psi_{trunk}$ daily variations are substantial. As tree growth is believed to occur mostly at night, when plant $\psi$ is highest due to reduced transpiration, we calculated daily $\psi_{trunk}$ and $T_{air}$ as nighttime (i.e. 22:00–5:00 CET) averages (Rossi et al., 2008; Steppe et al., 2015; but see Mencuccini et al., 2017) (Fig. 2).

In order to (1) test the suitability of $\psi_{soil}$ and $\psi_{trunk}$ as proxies of cambium $\psi$ and (2) test the relative weight of $T$ vs. $\psi$ to model sink limitation of intra- and inter-annual P, we ran five different model scenarios using the following input combinations: (MS1–$T_{air}$) $T_{air}$,
\[ \psi = \text{constant}; \text{ (MS2} - \psi_{\text{soil}}) \ T = \text{constant}, \ \psi = \psi_{\text{soil}}; \text{ (MS3} - \psi_{\text{trunk}}) \ T = \text{constant}, \ \psi = \psi_{\text{trunk}}; \text{ (MS4} - T_{\text{air}} + \psi_{\text{soil}}) \ T = T_{\text{air}}, \ \psi = \psi_{\text{soil}}; \text{ (MS5} - T_{\text{air}} + \psi_{\text{trunk}}) \ T = T_{\text{air}}, \ \psi = \psi_{\text{trunk}}. \]

The value of the constant variables was set to the average of the corresponding variable across the growing season.

Model simulations started on spring equinox (DOY 80), ended in late October (DOY 300) and were run independently for each species, year and plot. Model runs were restricted to the period 2009-2013 and the valley-bottom and South-facing plots (N13, S16, S19 and S22, Table S1) where the full series of xylogenesis, temperature and water potential were available. The model simulates daily CP. Simulated AP was calculated as the maximum CP at the end of each simulation and simulated APs was obtained by normalization of simulated AP as described for observed APs. Simulated CPr was calculated by dividing CP by AP and simulated P onset and cessation were calculated as the dates on which CPr equals 5% and 95%. Simulated PR and PRr were calculated from simulated CP and CPr, respectively, using a monthly time-step to match the definitions made for observations.

The two unknown model parameters \( \gamma_\psi \) and \( \gamma_T \) were estimated by model calibration against observed relative cumulative cell production, by minimization of the Sum of Squared Residuals (SSR), using the box-constrained L-BFGS-B algorithm implemented in the function ‘optim’ of the R package ‘stats’. Calibration was done independently for each model scenario, using CPr of the two first sampling years (2009-2010). In order to obtain sensible parameter estimates for both \( \gamma_T \) and \( \gamma_\psi \), and due to the low variability of soil water potential at higher elevations, we restrained model calibration to the low elevation plots (1300–1600 m), where we expected both \( T \) and \( \psi \) limitations, and used high elevation plots (1900–2200 m) for spatial validation.

Model validation was undertaken across years and elevations by comparing observed and simulated P phenology, PRr (excluding the calibration period 2009–2010) and APs, given the different model scenarios. For simplicity, in most of our analyses we aggregated sites into low (1300–1600 m) and high (1900–2200 m) elevations, and compare model performance between them. In the case of PRr, aggregated observations and simulations were averaged to improve data robustness. Goodness-of-fit statistics included the slope and the \( R^2 \) of the regression between observations and simulations, as well as the Akaike Information Criterion (AIC), the Root Mean Squared Error (RMSE) and bias defined as the average difference between
simulations and observations. Three months moving-window correlations between observed and simulated PRr were performed in order to explore the seasonal variation of the model’s ability to explain observed cambial activity. Last, MS1 was additionally run using a second set of parameters – MS1(P2) thereafter – where $\gamma_T$ was set to the species-specific values obtained by calibration of MS5. This was done to compare CP, PR and AP obtained using either MS1(P2) and MS5, in order to isolate the effect of $\psi_{trunk}$ on intra- and inter-annual P variability. Furthermore, we simulated P phenology using MS1(P2) in order to reflect the effect of the uncertainty surrounding $\gamma_T$ on this feature.
4. Results

4.1 Calibrated temperature and water potential yield thresholds

Parameter estimates obtained from calibration against relative cumulative P in 2009 and 2010 at the low elevation plots are shown in Table 2 for each model scenario. On average, the $T$ and $\psi$ yield thresholds for P ($\gamma_T$ and $\gamma_\psi$) were found to equal 6.6 °C and -1.1 MPa, respectively, which is close to commonly reported values (Rossi et al., 2007; Körner, 2008; Meinzer et al., 2008; Lempereur et al., 2015; Cabon et al., 2020). Species-specific variations were observed as $\gamma_T$ and $\gamma_\psi$ were about 1.5°C higher and 0.7 MPa lower, respectively, for larch than spruce. The RMSE and the $R^2$ of the regression between simulations and calibration data ranged between 4.5–20.5 and 0.88–0.99 depending on the model scenario, MS5–$T_{\text{air}}+\psi_{\text{trunk}}$ resulting in the best fit (Table 2, Fig. 3a and c).

4.2 Phenology of tracheid production

TP started on average on DOY 148 (late May), ended on DOY 237 (late August) and lasted 89 days (Fig. S6). P onset was delayed at higher elevations (1.5 days·100 m$^{-1}$, p<0.001) while P cessation was advanced at a lower rate, (-1.0 days·100 m$^{-1}$, p<0.05). As a result, P duration strongly shortened with elevation (-2.4 days·100 m$^{-1}$, p<0.001). Larch P phenology was delayed compared to spruce, with a later onset (5.0 days, p<0.05) and later cessation (5.7 days, p<0.05) than spruce, resulting in a similar P duration for both species ($\Delta t=0.6$ days, p=0.83).

Simulations of P phenology greatly differed between model scenarios (Fig. 4, Table S2). Scenarios that did not include $T$ as input (i.e. MS2–$\psi_{\text{soil}}$ and MS3–$\psi_{\text{trunk}}$) clearly failed at reproducing both P onset and cessation, with offsets of about two and one month, respectively. On the contrary, the scenario that included only $T$ (MS1–$T_{\text{air}}$) performed relatively well to simulate P onset, although estimates were negatively biased by two weeks, but failed to reproduce P cessation, with a positive bias of over one month. Including both $T$ and $\psi$ as drivers (MS4–$T_{\text{air}}+\psi_{\text{soil}}$ and MS5–$T_{\text{air}}+\psi_{\text{trunk}}$) yielded better estimates of P onset relative to MS1, as indicated by reduced bias and improved goodness-of-fit. MS1(P2) yielded similarly good estimates of P onset compared to MS4 and MS5. When considering P cessation, the two complete model scenarios performed better than those including either the effect of $T$ or $\psi$ alone.
However, MS4–T\textsubscript{air}+\psi\textsubscript{soil} was considerably less accurate at the high than at the low elevation plots, resulting in an overall lower performance of MS4 compared to MS5. Although MS5 was the best model to simulate P cessation, it only moderately explained the observed P cessation variance (R\textsuperscript{2}=0.3). MS1, MS4 and MS5 were further able to simulate the earlier P onset of spruce compared to larch (except MS5 at the high elevation plots) and MS4 and MS5 yielded species-specific differences in P cessation consistent with observations (except at the high elevation plots for MS4), although larch P cessation was overestimated.

4.3 Seasonal tracheid production

Observed cumulative relative P exhibited typical sigmoidal patterns, which varied from year-to-year and between elevations (Fig. 3 and detail by plot in Fig. S7). From these observations it appeared that larch and spruce CPR did not radically differ but larch CPR often lagged that of spruce, consistently with observed phenology. Transforming CPR into monthly-scale rates (PRr) yielded clear bell-shaped seasonal patterns and evidenced differences between elevations, years and species (Fig. 5). The data nevertheless tended to be noisier at the end of the growing season, often exhibiting fluctuating negative and positive PRr after DOY 250, when P was found to have already ended (Fig. 4).

All model scenarios yielded PRr estimates that were positively and significantly correlated to observations (Table S3). However, explained variance varied between 9% (MS2–\psi\textsubscript{soil}, high elevation) and 78% (MS5–T\textsubscript{air}+\psi\textsubscript{trunk}, low elevation), depending on model scenario and elevation (Fig. 6a, Table S3). Both at the high and low elevation plots, including T and \psi resulted in better models than when only one of the variables was included, as indicated by lower AIC values. Within single-variable model scenarios, MS3–\psi\textsubscript{trunk} performed best, followed by MS1–T\textsubscript{air} and MS2–\psi\textsubscript{soil}. Overall, the best-fitting model scenario was again MS5–T\textsubscript{air}+\psi\textsubscript{trunk}, which explained 71% of observed variance (all elevations pooled), and yielded little bias and deviation from the unity slope (Table S3). Simulations derived from MS5 closely matched rates and cumulative P (Fig. 3, Fig. 5) and largely reproduced species-specific differences. Using soil \psi in MS4–T\textsubscript{air}+\psi\textsubscript{soil} nevertheless increased model performance compared to using T\textsubscript{air} alone, and in the case of low elevation plots, MS4 performance was close
to that of MS5, as it explained 71% of observed variance and had similar bias, RMSE and deviation from the unity slope (Table S3).

Moving-window correlation between observed and simulated P rates (Fig. S8) revealed that, depending on the scenario, model explanatory power had pronounced seasonal fluctuations, the effect of \( T \) alone being able to explain most observed variance at the beginning of the growing season whereas \( \psi \) effect was strikingly more relevant during summer. Finally, the modelled interaction of both \( T \) and \( \psi \) was necessary to predict P rates at the end of the growing season.

When considering absolute P, taking into account the effect of \( \psi_{\text{trunk}} \) in addition to that of \( T_{\text{air}} \) (i.e. MS5 vs. MS1(P2); Fig. 7a) yielded comparable rates and cumulative P at the beginning of the growing season. However, differences appeared from c. DOY 190 on, as the inclusion of \( \psi_{\text{trunk}} \) in MS5 negatively affected P in comparison to MS1(P2) (see Fig. S9 for details by year) and resulted in a decrease of simulated AP by 35±28% on average (Fig. 7b). This difference showed large variations among years, ranging from -61% in 2011 and -6% in 2013, and was observed both at the low and the high elevation sites, although it was slightly larger on average in the former (-38% and -30%, respectively).

4.4 Annual tracheid production (AP)

Model success to reproduce AP was also dependent on the model scenario and elevation, and explained from 2 to 48% of the observed variance (Fig. 6b, Table S4). Although results were more variable, due to fewer observations, relative model performance across elevations and scenarios tended to be similar to the case of PRr (Fig. 6). Considering all elevations, the best-fitting model scenario was MS5–\( T_{\text{air}}+\psi_{\text{trunk}} \), which explained 43% of observed variance and had the lowest RMSE and departure from the unity slope, although MS3–\( \psi_{\text{trunk}} \), which had a lower \( R^2 \) also had a slightly lower AIC because of a lower number of parameters (Table S4). When considering only the low elevation plots, MS4 and MS5 yielded the best results, MS4 performing slightly better than MS5, although MS3 had the lowest AIC because of parameter number. At high elevations, MS3 was the best model scenario according to all statistics (\( R^2=0.48 \)), but MS5 had a similar explanatory power. In contrast, the other model scenarios did not yield significant linear relationships with observations at high elevations.
5. Discussion

Our results show that a tracheid production (P) model based on a mechanistic representation of the biophysical limitation of turgor-driven cambial activity by $T$ and $\psi$ can successfully reproduce observed patterns of softwood P. This result complements a previous study where turgor-driven tracheid enlargement outside of the cambium was modelled from $\psi$ (Cabon et al., 2020) and further illustrates the importance of turgor-driven cell expansion in wood formation (Steppe et al., 2015). More specifically, our model was able to successfully simulate both the phenology and the intra-annual dynamics of P, as well as, to a lower extent, inter-annual variability in P. Notably, the relative importance of $T$ and $\psi$ limitations varied little with elevation but dendrometer-derived $\psi_{\text{trunk}}$ outperformed $\psi_{\text{soil}}$ at high elevation plots. The model is conceptually disconnected from carbon assimilation and allocation (i.e. carbon sources), which allows focusing on processes directly controlling cambial activity (i.e. the carbon sink). Coupling our approach with carbon economy nevertheless appears promising for future model generalization.

5.1 Trunk water potential outperforms soil water potential to predict tracheid production

In this study we compared the significance of $\psi_{\text{soil}}$ and $\psi_{\text{trunk}}$, derived from soil moisture and dendrometer measurements, respectively, as proxies of cambium $\psi$ to predict cambial division. Plant $\psi$ is expected to equilibrate with $\psi_{\text{soil}}$ at night, when secondary growth is assumed to occur (Steppe et al., 2015; but see Mencuccini et al., 2017). However, nighttime transpiration and plant water storage depletion might, to some extent, prevent equilibration (Donovan et al., 2001; Bucci et al., 2004). Nighttime $\psi_{\text{trunk}}$ estimates based on dendrometer measurements at breast height were therefore expected to be more representative than $\psi_{\text{soil}}$ of the actual cambium $\psi$ (Dietrich et al., 2018). At the low elevation sites, $\psi_{\text{trunk}}$ closely followed variations in $\psi_{\text{soil}}$ under moderate drought conditions (Fig. 2), suggesting that $\psi_{\text{trunk}}$ was largely determined by $\psi_{\text{soil}}$, consistent with Oberhuber et al. (2015). At the high elevation plots, $\psi_{\text{trunk}}$ appeared to be decoupled from $\psi_{\text{soil}}$, which varied little, pointing out that under conditions of high water availability, other processes such as storage refilling and nighttime transpiration (observed
nighttime vapor pressure deficit increased with elevation) were responsible for $\psi_{trunk}$ variations. Overall, these results suggest that under mild soil water limitation such as the low elevation at our study site, $\psi_{soil}$ is a good proxy of actual plant $\psi$ and might be used to model plant cambial activity, but not under abundant soil water supply, where atmospheric water demand and plant water relations must be considered.

5.2 Relative importance of temperature and water potential

Wood formation at our study site (see also Moser et al., 2009; Cuny et al., 2019) showed a delayed onset with elevation, consistent with previously reported trends and the predictable effect of $T$ on the onset of wood formation (Jyske et al., 2014; Rossi et al., 2016; Zhang et al., 2018b; Delpierre et al., 2018), which was captured by our model (Fig. 4). Although in our model the dependence of $P$ on temperature was threshold-based, a minimum CP was required for considering that $P$ had started. Our approach was thus akin to a heat sum model (Delpierre et al., 2018), where heat accumulation is modulated by enzymatic activity and turgor pressure, rather than a simple threshold model. Taking into account the effect of chilling temperatures on endo-dormancy release might nevertheless be necessary to better account for contrasting thermal requirements between sites (Delpierre et al., 2018; Cuny et al., 2019). At the beginning of the growing season, the rate of $P$ further appeared to be mostly related to $T$, consistent with observed correlations between cambial activity and short-term $T$ variations (Deslauriers & Morin, 2005; Gruber et al., 2009; Luo et al., 2018). We also report an earlier $P$ cessation with elevation, although the trend was less pronounced. In contrast with growth onset, it is less clear which environmental factors might control growth cessation (Moser et al., 2009; Rossi et al., 2016; Cuny et al., 2019). It has been noted that despite low $T$ has the potential to induce $P$ cessation (Begum et al., 2018), $P$ often ends when $T$ is not limiting yet, thus allowing last formed tracheids to complete maturation under favorable conditions (Rossi et al., 2007). Our model estimates that if $P$ were limited by $T$ only, $P$ cessation would occur c. 40 days later than is observed (Fig. 4, Table S2), suggesting that $T$ is not the (only) factor triggering $P$ cessation. On the other hand, we observed that the correlation between PR and $T$ rapidly tended towards zero in early summer (DOY 180). Luo et al. (2018) also observed a reduced sensitivity of $P$ to $T$ after the peak of radial growth around summer solstice (DOY 172), which was attributed to photoperiod. Among environmental factors, photoperiod is commonly hypothesized to be the
cue controlling peak growth rate, eventually setting the end of wood formation in temperate, boreal or alpine climates (Rossi et al., 2006; Jackson, 2009; Cuny et al., 2015). Our observations, however, do not support the hypothesis that maximum day length determines the date of maximum growth rate, as peak P was delayed with elevation (Fig. S6a). Our modelling results further suggest that at our study site, $\psi$ becomes the main driver of PR during summer, whereas at the end of summer, $T$ and $\psi$ co-limit PR and eventually trigger P cessation. The onset of water limitation of cambial activity during summer thus likely explains the occurrence of maximum PR close to summer solstice and the lack of correlation between P and $T$ after that, as well as the early P cessation. These results indicate that drought may interact with $T$ to trigger wood formation cessation in our study area, similarly to Mediterranean systems where strong water limitation can dictate a pause or the end of wood formation (Vieira et al., 2014; Lempereur et al., 2015; Cabon et al., 2018). However, other explanations are possible and the hypothesis of a concomitant direct effect of photoperiod cannot be rejected.

Model analyses suggest that $\psi$ strongly constrained PR during summer relative to the potential growth theoretically allowed by $T$, independent of elevation (Fig. 7a, Fig. S9). Despite the occurrence of sustained water limitation on wood formation throughout a large part of the growing season is unexpected at a cold treeline, these results are consistent with other studies on wood phenology of high elevation vegetation of the Tibetan plateau (Ren et al., 2018; Zhang et al., 2018a) and the effect of precipitations and tree water status on xylogenesis and intra-annual diameter growth even in relatively humid and cold environments (Zweifel et al., 2006; Eilmann et al., 2011; D’Orangeville et al., 2013).

The capacity of the model to predict intra-annual P dynamics spread, to a certain extent, to the inter-annual scale, suggesting that annual wood formation of spruce and larch at our study site was partially controlled by the biophysical limitations of $T$ and $\psi$ on daily cambial activity. Consistently with the observed response of intra-annual P to environmental variables, AP was thus best explained by the interaction of both $T$ and $\psi$ effects (Fig. 6b). Regardless of site elevation, the effect of $T$ alone was a surprisingly poor predictor of annual growth, given the well-known effect of $T$ on tree growth in cold environments (Briffa et al., 1995; Luckman et al., 1997; D’Arrigo et al., 2001; Vaganov et al., 2006). The control of $T$ on tree growth commonly switches from positive to negative from cold toward hotter environments, as a
consequence of the effect of increasing $T$ on drought stress. (Martinez-Vilalta et al., 2008; King et al., 2013b; Peters et al., 2017; Klesse et al., 2018). Ongoing climate warming at our study site (King et al., 2013b) might therefore have resulted in a reduced sensitivity of recent tree growth to $T$ (Briffa et al., 1998; D’Arrigo et al., 2008). We calculated that on average, $\psi$-induced growth limitation accounted for a 35% reduction of AP, ranging from 61% in the driest year (2011–543 mm) to 6% only in the wettest (2013–941 mm) (Fig. S9). AP was found to be less limited by $\psi$ at the higher elevation plots, consistent with expectations (Littell et al., 2008). But the difference was relatively small and $\psi$ nonetheless induced a 30% growth reduction at the high elevation plots. These results thus question the hypothesis that climate warming should improve tree growth in cold environments such as treelines (e.g. Grace et al., 2002). Tree growth in regions where $T$ has been long regarded as the main climatic limitation might indeed become increasingly limited by warming-induced increased atmospheric water demand (Briffa et al., 1998; Piao et al., 2014; Babst et al., 2019).

### 5.3 Implications for wood formation modelling

The tracheid production model presented here is based on the assumption that $T$ and $\psi$ directly control wood formation through cambial activity, without considering photosynthesis and carbon allocation, thus adopting the sink-limitation perspective of tree growth proposed by Fatichi et al. (2014, 2019). Despite we acknowledge tree growth to be controlled by multiple factors such as photo-assimilates, nutrients, hormones and sugar signaling, which are the object of detailed models (e.g. Hölttä et al., 2010; Drew & Downes, 2015; Hartmann et al., 2017), here we only considered the biophysical effect of $T$ and $\psi$ on cambial cell enlargement and division. The model predictions (particularly scenario MS5) agreed well with observed P phenology, intra- and inter-annual P, across species and elevations. Furthermore, the model is parsimonious and grounded in a strong theoretical basis. Last, the model has only two free parameters, which were estimated by calibration and are consistent with the literature. Therefore, we argue that the direct effect of $T$ and $\psi$ on sink activity has a preponderant role in controlling wood formation at our study site. This conclusion is in line with accumulating empirical evidence that tree growth is increasingly sink-limited near the treeline (Körner, 2015). Further developments are nonetheless required as our model merely accounted for half of observed AP variance, suggesting that other factors, e.g. long-term tree carbon balance, likely
interact with direct environmental control on cambial activity to determine growth variability across years (Guillemot et al., 2015).

Our results also advocate for plant water relations as an important driver of cambial activity, independent of soil water supply. Tree water status sensitivity to atmospheric water demand at the treeline might be exacerbated by overall greater hydraulic constraints in cold environments due to increased water viscosity (Cochard et al., 2000), reduced root aquaporin activity (Wan et al., 2001) and reduced xylem hydraulic efficiency (Petit et al., 2011) resulting from low $T$.

Coupling sink processes with plant water and carbon economy holds great promise for modelling global vegetation responses to future climate and rising [CO$_2$]. It would be relatively straightforward to extend the model presented here to explicitly simulate tracheid lumen and wall dimensions (Carteni et al., 2018; Cabon et al., 2020), which would allow quantifying tree growth in terms of volume and biomass increment, as well as incorporating feedbacks on hydraulic and water relations (Mencuccini et al., 2019). Implementing these processes within DGVMs will likely help reducing the uncertainty concerning the fate of the terrestrial carbon sink.
6. Acknowledgements

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7. Authors contribution

AC, MC and JMV had the original idea of the research question and designed the study with the help of PF and RLP. PF and RLP realized the setting design, fieldwork and sample processing. AC developed the model, realized the analyses and wrote the manuscript with contributions from all coauthors.


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Zweifel R, Item H, Häsl er R. 2001. Link between diurnal stem radius changes and tree water

9. Tables

Table 1. Tracheid production model symbols and abbreviations. The value of fixed model parameters are given in parenthesis, alongside with the units. The scaling parameter A was calculated such that $\phi(T)$ (Eq. 4) varies between 0 and $\phi_{\text{max}}$. Parameter $\phi$ from Cabon et al., 2020 corresponded to $T=15$ °C and was corrected to $T=30$ °C to obtain $\phi_{\text{max}}$, based on Eq. 4.

<table>
<thead>
<tr>
<th>Name</th>
<th>Units (value)</th>
<th>Signification</th>
<th>Observation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\psi$</td>
<td>MPa</td>
<td>Water potential</td>
<td>State variable</td>
</tr>
<tr>
<td>$T$</td>
<td>°C</td>
<td>Temperature</td>
<td>State variable</td>
</tr>
<tr>
<td>$r$</td>
<td>day$^{-1}$</td>
<td>Relative cell volume increment</td>
<td>Intermediate variable</td>
</tr>
<tr>
<td>$\phi$</td>
<td>MPa$^{-1}$ day$^{-1}$</td>
<td>Cell wall extensibility</td>
<td>Intermediate variable</td>
</tr>
<tr>
<td>$\gamma_\psi$</td>
<td>MPa</td>
<td>Water potential yield threshold</td>
<td>Calibrated parameter</td>
</tr>
<tr>
<td>$\gamma_T$</td>
<td>°C</td>
<td>Temperature yield threshold</td>
<td>Calibrated parameter</td>
</tr>
<tr>
<td>$\phi_{\text{max}}$</td>
<td>MPa$^{-1}$ day$^{-1}$ (0.61)</td>
<td>Maximum cell wall extensibility</td>
<td>Fixed parameter, Cabon et al. 2020, corrected for temperature</td>
</tr>
<tr>
<td>$R^*$</td>
<td>J mol$^{-1}$ K$^{-1}$ (8.314)</td>
<td>Ideal gas constant</td>
<td>Fixed parameter</td>
</tr>
<tr>
<td>$A$</td>
<td>K$^{-1}$ (5.36$\cdot10^{12}$)</td>
<td>Scaling parameter (derived from other parameters)</td>
<td>Fixed parameter; calculated</td>
</tr>
<tr>
<td>$\Delta H_A$</td>
<td>J mol$^{-1}$ (87.5$\cdot10^{3}$)</td>
<td>Enthalpy of activation of the enzymatic system</td>
<td>Fixed parameter; Parent et al., 2010</td>
</tr>
<tr>
<td>$\Delta H_D$</td>
<td>J mol$^{-1}$ (1.09$\cdot10^{3}$)</td>
<td>Enthalpy difference between the catalytically active and inactive states of the enzymatic system</td>
<td>Fixed parameter; Parent et al., 2010</td>
</tr>
<tr>
<td>$\Delta S_D$</td>
<td>J mol$^{-1}$ K$^{-1}$ (333$\cdot10^{3}$)</td>
<td>Entropy difference between the catalytically active and inactive states of the enzymatic system</td>
<td>Fixed parameter; Parent et al., 2010</td>
</tr>
<tr>
<td>$T_{\text{opt}}$</td>
<td>°C (30)</td>
<td>Temperature of maximum enzymatic activity (derived from other parameters)</td>
<td>Fixed parameter; calculated</td>
</tr>
<tr>
<td>$N_c$</td>
<td>(8.85)</td>
<td>Number of cambial cells able to divide</td>
<td>Fixed parameter; measured</td>
</tr>
<tr>
<td>PR</td>
<td>day$^{-1}$</td>
<td>Tracheid production rate</td>
<td>Primary output</td>
</tr>
<tr>
<td>Abbreviation</td>
<td>Unit</td>
<td>Description</td>
<td>Validation</td>
</tr>
<tr>
<td>--------------</td>
<td>------</td>
<td>-------------</td>
<td>------------</td>
</tr>
<tr>
<td>PRr</td>
<td>% day$^{-1}$</td>
<td>Relative tracheid production rate</td>
<td>Secondary output (validation)</td>
</tr>
<tr>
<td>CP</td>
<td></td>
<td>Cumulative tracheid production (i.e. PR cumulative sum)</td>
<td>Secondary output</td>
</tr>
<tr>
<td>CPr</td>
<td>%</td>
<td>Relative cumulative tracheid production</td>
<td>Secondary output (validation)</td>
</tr>
<tr>
<td>AP</td>
<td></td>
<td>Annual tracheid production (i.e. CP at the end of the year)</td>
<td>Secondary output</td>
</tr>
<tr>
<td>APs</td>
<td></td>
<td>Standardized annual tracheid production</td>
<td>Secondary output (validation)</td>
</tr>
<tr>
<td>P onset</td>
<td>DOY</td>
<td>Onset of tracheid production</td>
<td>Secondary output (validation)</td>
</tr>
<tr>
<td>P peak</td>
<td>DOY</td>
<td>Day of maximum tracheid production rate</td>
<td>Secondary output (validation)</td>
</tr>
<tr>
<td>P end</td>
<td>DOY</td>
<td>End of tracheid production</td>
<td>Secondary output (validation)</td>
</tr>
</tbody>
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Table 2. Calibrated model parameters for the different model scenarios and summary statistic of the calibration fit. RMSE is the root mean squared error. $R^2$ is calculated using a linear regression between observations and simulations.

<table>
<thead>
<tr>
<th>Model scenario</th>
<th>Species</th>
<th>$\gamma_T$ (°C)</th>
<th>$\gamma_\psi$ (MPa)</th>
<th>RMSE (%)</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS1–$T_{air}$</td>
<td>Larch</td>
<td>4.9</td>
<td>9.7</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>2.9</td>
<td>16.8</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td>MS2–$\psi_{soil}$</td>
<td>Larch</td>
<td>-2.08</td>
<td>17.7</td>
<td>0.93</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>-0.84</td>
<td>20.5</td>
<td>0.89</td>
<td></td>
</tr>
<tr>
<td>MS3–$\psi_{trunk}$</td>
<td>Larch</td>
<td>-1.65</td>
<td>19.2</td>
<td>0.93</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>-0.90</td>
<td>20.4</td>
<td>0.91</td>
<td></td>
</tr>
<tr>
<td>MS4–$T_{air}+\psi_{soil}$</td>
<td>Larch</td>
<td>8.7</td>
<td>-0.74</td>
<td>5.0</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>8.4</td>
<td>-0.43</td>
<td>8.3</td>
<td>0.96</td>
</tr>
<tr>
<td>MS5–$T_{air}+\psi_{trunk}$</td>
<td>Larch</td>
<td>8.4</td>
<td>-1.22</td>
<td>4.5</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>6.2</td>
<td>-0.87</td>
<td>6.3</td>
<td>0.98</td>
</tr>
</tbody>
</table>
Fig. 1. Modelled tracheid production rate (PR) as a function of (a) water potential and (b) temperature as given by Eq. 5 in the main text, given $\gamma_T = 7 \, ^\circ\text{C}$ and $\gamma_\psi = -1 \, \text{MPa}$ (black lines; the grey line represents the effect of temperature without threshold). $T_{\text{opt}} = 30 \, ^\circ\text{C}$ is derived from the fixed parameter values in Eq. 4 (Table S1). Here PR is relativized by the maximum PR given the range of water potential and temperature.
Fig. 2. Time series of the model inputs at the different plots used for model simulations (N13, S16, S19 and S22): soil water potential ($\psi_{\text{soil}}$, black dashed lines), nighttime trunk water potential ($\psi_{\text{trunk}}$) of larch (red) and spruce (blue) and nighttime air temperature ($T_{\text{air}}$, grey). Periods used for model simulations (i.e. from DOY 80 to 300) are denoted by a white background.
Fig. 3. Observed (points and dotted lines) and simulated (solid lines) cumulative relative tracheid production (CPr) of larch (red) and spruce (blue) at the low (1300-1600 m) and high elevation (1900-2200 m) plots, for the period 2009–2013. Light grey background denotes the data used for model calibration (low elevation plots on the period 2009-2010, panels a and c). Model simulations correspond to the model scenario MS5–T_{air}+ψ_{trunk}. Detailed observations and simulations per plot are available in Fig. S7.)
Fig. 4. Observed (empty symbols and dashed lines) and simulated (filled symbols and solid lines) dates for onset (circles), peak (triangles) and cessation (squares) of tracheid production (P) for larch (red) and spruce (blue) as average over the period 2009-2013 at the high and low elevation plots, given the different model scenarios. Note that only larch is present at the treeline and that high elevation only includes one plot in the case of spruce. See Fig. S6 for observed phenology by individual elevations and on the full extent of xylogenesis sampling. Stars indicate model simulations with MS1(P2). Points and error-bars are means and bootstrapped 95% confidence interval.
Fig. 5. Seasonal relative tracheid production rate (PRr; observed – empty dots and dashed lines – and simulated – solid lines) for larch (red) and spruce (blue) at the high and low elevation plots over the period 2009-2013. Light grey background denotes the plots and years used for model calibration (Low elevation plots over the period 2009-2010, panels a and c). Simulations correspond to the model scenario MS5–Tair+ψtrunk.
Fig. 6. $R^2$ of the regression between observed and simulated (a) relative production rate (PRr) over the period 2011-2013 (2009-2010 being the calibration period) and (b) standardized annual production (APs) over the period 2009-2013. Results are shown for all plots (dark grey) as well as at the low (medium grey) and high (light grey) elevation plots. Simulations were run using the different Model Scenarios (MS) where $T_{\text{air}}$, $\psi_{\text{soil}}$, $\psi_{\text{trunk}}$ are used as alone (setting either $T$ or $\psi$ constant) or in paired combination. Statistical significance of regressions is coded as follows: ns–p>0.1; – p<0.1; * – p<0.05; ** – p<0.01; *** – p<0.001.
Fig. 7. (a) Simulated absolute rate (shaded areas) and cumulative (lines) production (PR and CP) at the low and high elevation plots, given the two model scenarios MS1(P2) and MS5 and averaged across years (2009–2013). (b) Relative difference in annual tracheid production (AP) as simulated with model scenario MS5–Tair+ψtrunk compared to MS1(P2)–Tair. Columns are means and error bars are 95% bootstrapped confidence interval.