RESEARCH ARTICLE

Tree growth in Switzerland is increasingly constrained by rising evaporative demand

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Abstract

1. The response of trees to intra-annual environmental constraints varies temporally throughout a growing season and spatially across landscapes. A better understanding of these dynamics will help us anticipate the impacts of short-term climate variability and medium-term climate change on forests. Using the process-based 3-PG forest ecosystem model, we assessed the spatial manifestation and seasonal variation in environmental constraints [vapour pressure deficit (VPD), air temperature and soil water availability] on tree growth for the potential distribution range of seven widespread Central European tree species.

2. We focused our analyses on Switzerland, where large climatic gradients occur within a comparatively small geographic area. On average, over the last 60 years, simulated forest growth during the May–August growing season was limited by high VPD (67% of the forested area), low air temperature (29%) or low soil water availability (4%). But this response varied among species and across elevations.

3. When comparing the period 1961–1990 with 1991–2018, we observed major shifts from former temperature limitation to recent VPD limitation across 12% of the area (3%–25%, depending on species), mainly at mid-elevations (700–1,200 m a.s.l.). At the same time, forest growth at lower elevations (i.e. below 700 m a.s.l.) became more limited by available soil water at the end of the growing season.

4. *Synthesis*. Our results highlight how the relative impact of environmental growth constraints has shifted in the last three decades, and show that the importance of VPD as a dominant environmental growth constraint has increased for tree species in Swiss and Central European forests. Understanding the spatial and temporal variability in environmental growth constraints will help to generate accurate

species-specific risk maps for forest managers to identify areas with elevated drought and heat stress in the near future.

1 | INTRODUCTION

With global warming, trees are increasingly exposed to environmental conditions outside their optimal range, including higher average air temperature, rising evaporative demand (i.e. increasing vapour pressure deficit, VPD) and low soil water availability (Allen et al., 2015; Gharun et al., 2020; Morales-Castilla et al., 2020; Pachauri et al., 2014; Williams et al., 2013). These alterations in environmental conditions have led to important changes in forest dynamics and distribution, including a vegetation shift to higher elevation and/or latitudes (Lamprecht et al., 2018; Rees et al., 2020), large-scale die-off events at the dry edge of species' distribution ranges (Hartmann et al., 2015), reduced primary productivity (Trotsiuk, Hartig, Cailleret, et al., 2020), and a general shift towards younger stands with a faster generation turnover (McDowell et al., 2020). Understanding and predicting forest ecosystem responses to climate change drivers such as continuously rising temperatures and transient disturbances such as heatwaves and drought events is thus essential for managing forests towards greater resistance and resilience, as well as for estimating changes in future forest carbon budgets and biodiversity (Clark et al., 2011; Pilotto et al., 2020; Thom et al., 2017).

Previous studies have identified that tree growth is primarily limited by temperature and growing season length in cold-humid climates (Churkina & Running, 1998; St. George & Ault, 2014). This paradigm is widely accepted. However, it is less clear if and where this temperature–growth relationship remains stable during the whole growing season or if it is seasonally affected (weakened or strengthened) by soil water availability limitations on tree growth. Moreover, in recent years, several studies have highlighted that rising VPD is increasingly limiting plant growth in many biomes, sometimes to a greater extent than soil water availability and temperature (Babst et al., 2019; Williams et al., 2013). For example, using projections from ten general circulation models, Novick et al. (2016) suggested that VPD could account for more than 70% of the growing season limitation on evapotranspiration in temperate forests by the end of the century. However, whether recent trends in VPD have already affected forest growth throughout the growing season, and how this impact may vary across species, remains unknown.

The foundations for understanding tree growth responses to environmental constraints were established by spatially extensive and temporally highly resolved dendro-ecological studies (e.g. based on measurements of tree-ring width/density, wood anatomy, xylogenesis, stable isotopes), starting in the 20th century (Fritts, 1976). In more recent years, advances in wood anatomy and xylogenesis research have helped to identify the timing and duration of cell formation and maturation, and subsequently the environmental constraints regulating those processes (Cuny & Rathgeber, 2016; De Micco et al., 2019; Rathgeber et al., 2016). Yet, such sub-seasonal assessments of tree growth are relatively recent and do not yet span large environmental gradients, in part, because they are comparatively time-consuming and costly. Furthermore, part of the difficulty in empirically identifying the impacts of climatic drivers on forest growth is that multiple drivers tend to co-occur and interact, making it difficult to disentangle their relative importance (Feichtinger et al., 2015). For instance, high VPD conditions usually occur in nature concurrently with other stresses such as heatwaves and soil droughts that are generally regarded as primary disturbances of plant functions (Gharun et al., 2020; Grossiord et al., 2020).

Advances in the parametrization and validation of dynamic vegetation models (DVMs) have positioned them as increasingly reliable tools for predicting and projecting forest growth under novel climatic conditions (Zuidema et al., 2018). While studies based on calibrated DVMs have uncovered spatial and temporal variations in forest productivity along large environmental gradients, they have rarely addressed variation in growth rates and the relative importance of environmental growth constraints at fine spatial resolution (~1 km^2). This is, in part, because many DVMs have relatively simplistic schemes of disentangling the impact of climatic factors on growth (Sitch et al., 2015), which challenges sub-seasonal assessments of tree growth and its climatic drivers (Babst et al., 2021).

In this study, we examine how the growth responses of seven major European tree species (*Larix decidua* Mill., *Picea abies* (L.) H. Karst, *Abies alba* Mill., *Fagus sylvatica* L., *Acer pseudoplatanus* L., *Pinus sylvestris* L. and *Quercus robur* L.) to environmental constraints (VPD, temperature and soil water content) vary throughout the growing season along a 2,000-m elevational gradient in Switzerland, which represents a 15°C range of mean annual temperatures and a 2,000 mm range of annual precipitation. To achieve our goal, we used intensive computer simulations of the process-based forest ecosystem model 3-PG (Physiological Principles Predicting Growth; Landsberg & Waring, 1997) to simulate monthly resolved environmental constraints on forest growth. The 3-PG model has previously been calibrated with 1,123 permanent forest monitoring plots (Forrester et al., 2021; Trotsiuk, Hartig, Cailleret, et al., 2020) spanning the period from 1930 to 2018 across the large environmental gradients that occur in Switzerland. We further complemented our process-based model analysis with spatially explicit empirical estimations from tree-ring chronologies previously published in Babst et al. (2019). Specifically, we address the following questions: (a)

How do the impacts of environmental constraints (VPD, temperature and soil water) on forest growth change within a growing season and along an elevational gradient, and (b) How did the relative importance of the different environmental constraints change due to recent climate change (1961–1990 vs. 1991–2018)?

2 | MATERIALS AND METHODS

2.1 | Dynamic vegetation model

3-PG is a process-based forest ecosystem model that consists of five sub-models, starting with light absorption and assimilation, and ending with the conversion of biomass into output variables (Forrester & Tang, 2016; Landsberg & Waring, 1997; Sands & Landsberg, 2002). It is a cohort-based, non-spatially explicit model with a monthly time step. During each time step of the simulation, 3-PG calculates the environmental constraints that control forest growth. Environmental constraints include responses to soil water, atmospheric VPD, air temperature and frost, and are normalized on a continuous scale from 0 (full constraint, no growth) to 1 (no constraint). Suboptimal temperatures, high VPD, infertile soils and low available soil water limit photosynthesis and affect forest growth and allocation of dry mass.

The temperature constraint is based on species-specific minimum, optimal and maximum temperatures required for growth, and typically has a unimodal shape with a peak (no growth limitation) at the optimum temperature (Sands & Landsberg, 2002). Growth potential declines exponentially with increasing VPD and is influenced by a species-specific parameter that quantifies the stomatal response to VPD (Landsberg & Waring, 1997). The soil water modifier follows a sigmoidal curve as a function of relative available soil water, which changes shape with soil texture (Landsberg & Waring, 1997). We focus on those environmental constraints because they were previously used to identify tree species vulnerabilities to environmental drivers in 3-PG at larger scales in western North America (Mathys et al., 2017) and Brazil (Almeida et al., 2010). The atmospheric CO_2 concentration was considered as forcing data for model simulation. We, however, did not focus our analyses on the CO_2 concentration due to low spatial variation and relatively limited seasonal changes.

2.2 | Model simulations

For our simulations, we used a re-implementation of the 3-PG model programmed in Fortran 95 and wrapped into an R package R3PG (Trotsiuk, Hartig, & Forrester, 2020). The model's species-specific parameters were derived from previous calibrations of 3-PG performed for Switzerland (Forrester et al., 2021; Trotsiuk, Hartig, Cailleret, et al., 2020). The 3-PG model was driven with time series of spatially interpolated monthly meteorological data. The interpolation (100-m spatial resolution) of the meteorological data was conducted by the Landscape Dynamics group (WSL, Switzerland) using data from MeteoSwiss stations (Swiss Federal Office of Meteorology

and Climatology) by employing the DAYMET method (Thornton et al., 1997). Site-specific information on soil type and plant-available soil water was retrieved from European soil database-derived data (Panagos et al., 2012).

We simulated environmental growth constraints for the species' potential distribution ranges within the forested area of Switzerland (Zimmermann et al., 2014) on a 1 × 1 km grid for seven dominant tree species: *Larix decidua*, *Picea abies*, *Abies alba*, *Fagus sylvatica*, *Acer pseudoplatanus*, *Pinus sylvestris* and *Quercus robur*. For this purpose, we simulated the growth of these tree species in monocultures with the average climate observed during 1961–1990 or 1991–2018. The stands were initialized as 2-year-old plantations with an initial density of 2,500 trees/ha and simulated until the age of 30 years.

For each simulated month, we obtained the relative contribution of environmental constraints (VPD, temperature and soil water) on tree growth. We first identified the most limiting environmental constraint among the three selected for each month as the one which, on average, had the lowest value (highest constraints on growth) during the simulation period (30 years). For each of the simulated grid cells, we further selected the environmental constraint that was dominant during most of the months during the growing season (May-August). The May–August growing season was selected based on a previous analysis of tree growth in Switzerland, when most of the cumulative annual growth (more than 95%) occurs within this period (Cuny et al., 2019). We fitted a generalized additive model to evaluate the change in environmental constraints along the elevational gradient. For this purpose, we excluded grid cells falling into the lowest 2.5% or highest 2.5% of the density distribution of the potential species habitat along the elevational gradient.

2.3 | Tree-ring climate space

We evaluated the most limiting environmental constraint for tree growth at a given location as simulated by the 3-PG model using empirically derived results of climate-growth relationships. For this purpose, we used the spatially explicit dataset from Babst et al. (2019), who projected cumulative monthly climate correlations from a global tree-ring network into climatic and geographic space. This dataset, compiled from a mixed-species network (including seven species used in this study), is derived from 2,710 tree-ring sites and contains response maps for VPD, temperature and precipitation. We resampled the Babst et al. (2019) climate response surfaces for Switzerland based on the growing season (May–August) temperature and annual precipitation of each DAYMET grid cell. This yielded spatially resolved results of the annual cumulative absolute covariances (positive or negative) between climate and tree growth during the reference period (1961–1990) and the warmer period (1991–2018) that we then compared with the respective results provided by the 3-PG model. The output of Babst et al. (2019) however, does not allow for the distinction of species-specific differences in climate response, nor for sub-seasonal changes in the dominant limiting factors.

3 | RESULTS

3.1 | Environmental growth constraints: Within-season and elevational gradients

Forest growth was mainly limited by high VPD and low temperature for the simulated stands (Figure 1). There was a continuous transition from cold temperature limitation at higher elevations to limitation by high VPD at lower elevations for all simulated tree species. On average, growth across the potential species distribution areas was most strongly limited to 67% (43%–96%) by high VPD, to 29% (3%–56%) by low temperature, and only to 4% (0%–5%) by low soil water availability during the simulated periods. Tree-ring analysis revealed that, on average, growth across the potential species distribution areas was limited to 69% by high VPD, to 30% by low temperature, and only to 1% by precipitation during the simulated period.

We found significant seasonal changes in how environmental constraints limited growth throughout the growing season. At the beginning of the growing season, most of the species were limited by cold temperatures, independent of elevation. As the seasons progressed, this limitation changed to high VPD and in some small areas also to low soil water availability, mainly at lower elevations (Figure 2).

3.2 | Changes in environmental constraints due to recent warming

The 3-PG model simulations indicated a substantial change in the dominant environmental constraints during the more recent warmer period (1991–2018) compared to the reference period (1961–1990; Figure 3). On average, the observed changes simulated by the 3-PG model occurred on 10% of the potential species distribution areas, which is slightly higher compared to results derived from the tree-ring analysis (7%). The largest changes of 14% (2%–30%, depending on the species) occurred at the beginning of the growing season (May), when formerly low temperature limitation was replaced by recent high VPD limitation. This change mostly affected the spatial distribution of growth constraints for *Q. robur* (30%), *P. abies* (20%) and *A. alba* (14%). The majority of shifts early in the growing season occurred at lower elevations (~700 m a.s.l.) due to warmer and drier springs. By the end of the growing season (August), approximately 11% (1%–24%) of the area exhibited changes in the dominant environmental growth constrains. Seasonal changes mainly affected *P. abies* (24%), *F. sylvatica* (19%) and *L. decidua* (15%). Shifts at the end of the growing period mainly occurred at higher elevations (~1,200 m a.s.l.) due to the longer, warmer and drier summer periods. Based on the tree-ring analysis, the change in limiting environmental constraints occurred on average at 1,300 m a.s.l. (*SD* = 344 m). Changes in environmental constraints of coniferous tree species (*L. decidua*, *A. alba*, *P. sylvestris*) showed much less evident signals compared to broadleaved tree species.

4 | DISCUSSION

The calibrated forest ecosystem model 3-PG agreed well with the climate space from the global tree-ring dataset (Figure S1) and allowed for the quantitative modelling of environmental constraints
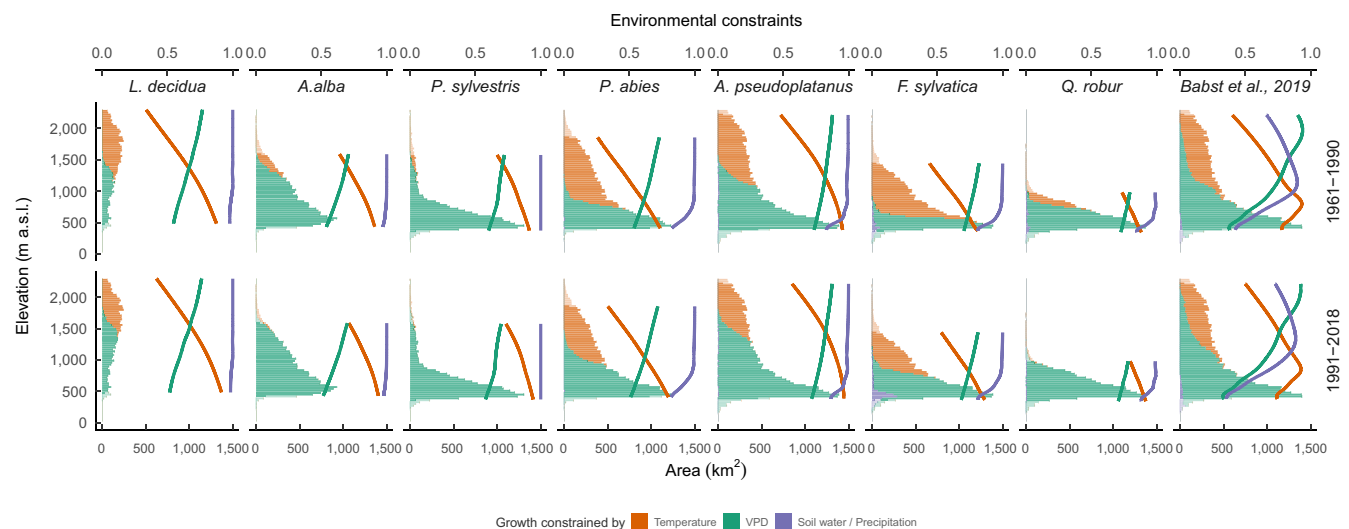

FIGURE 1 Prevailing environmental constraints during the growing season (May–August) along the elevation gradient (30-m bins) for each species. Lines represent the average value (0 - full constraint; 1 - no constrain) of environmental constraints along the elevational gradient. Cumulative histograms indicate the absolute area for a given species at a given elevation affected most by a particular environmental constraint. Light colour areas on the histogram show the grids outside the 95% distribution range. The most right panel indicates the distribution of dominant climatic drivers showing the highest correlation with tree-ring width from Babst et al. (2019). Lines represent the inverse cumulative correlations (0-maximum correlation; 1-no correlation) over the course of 16 months [1-abs (cumulative correlation)] between climate drivers and tree-ring width index (see methods for details)
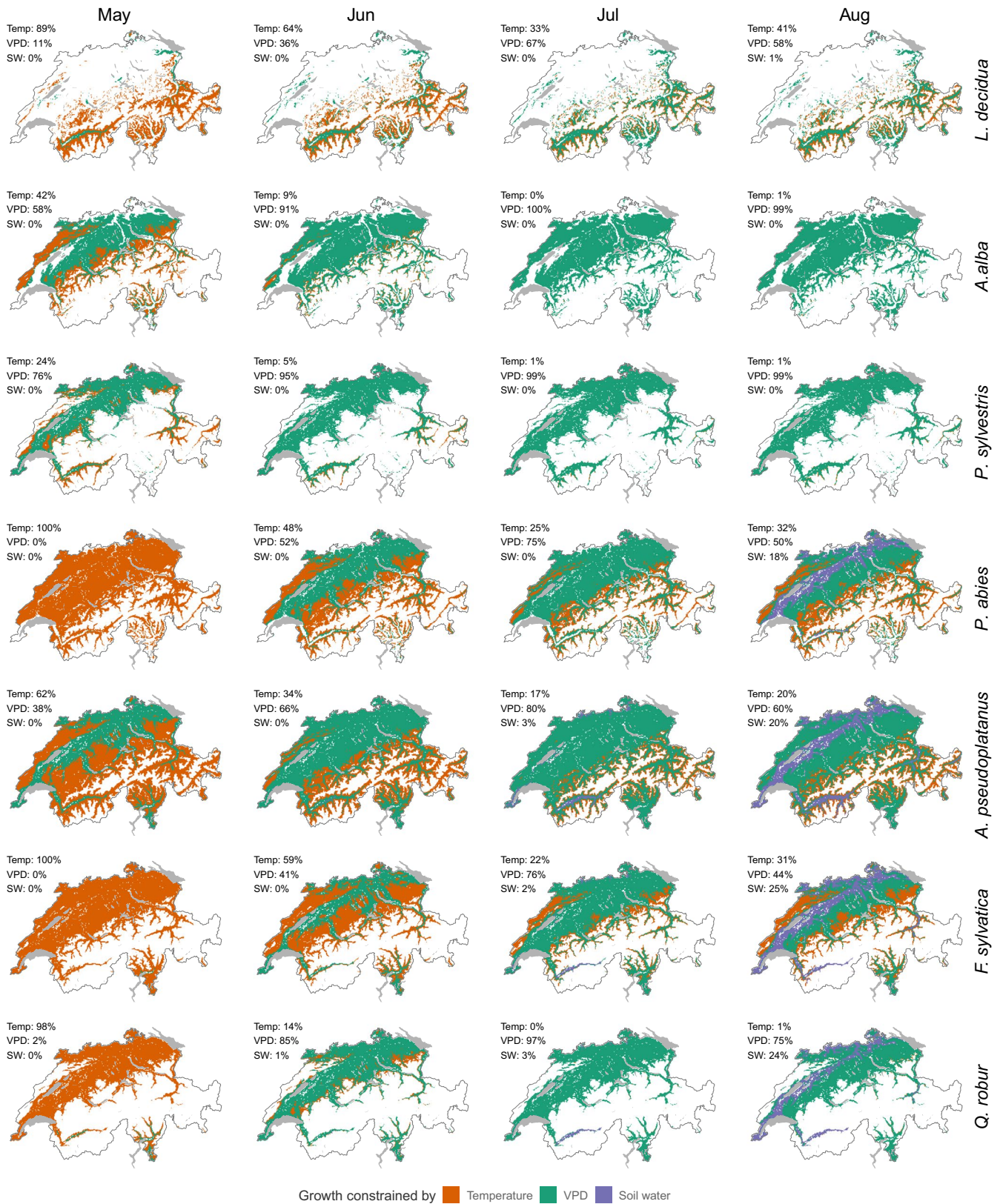
FIGURE 2 Seasonal changes in the spatial distribution of simulated environmental constraints during the 1961–1990 period. Numbers indicate the percentage of grid cells where the respective environmental constraint is prevailing
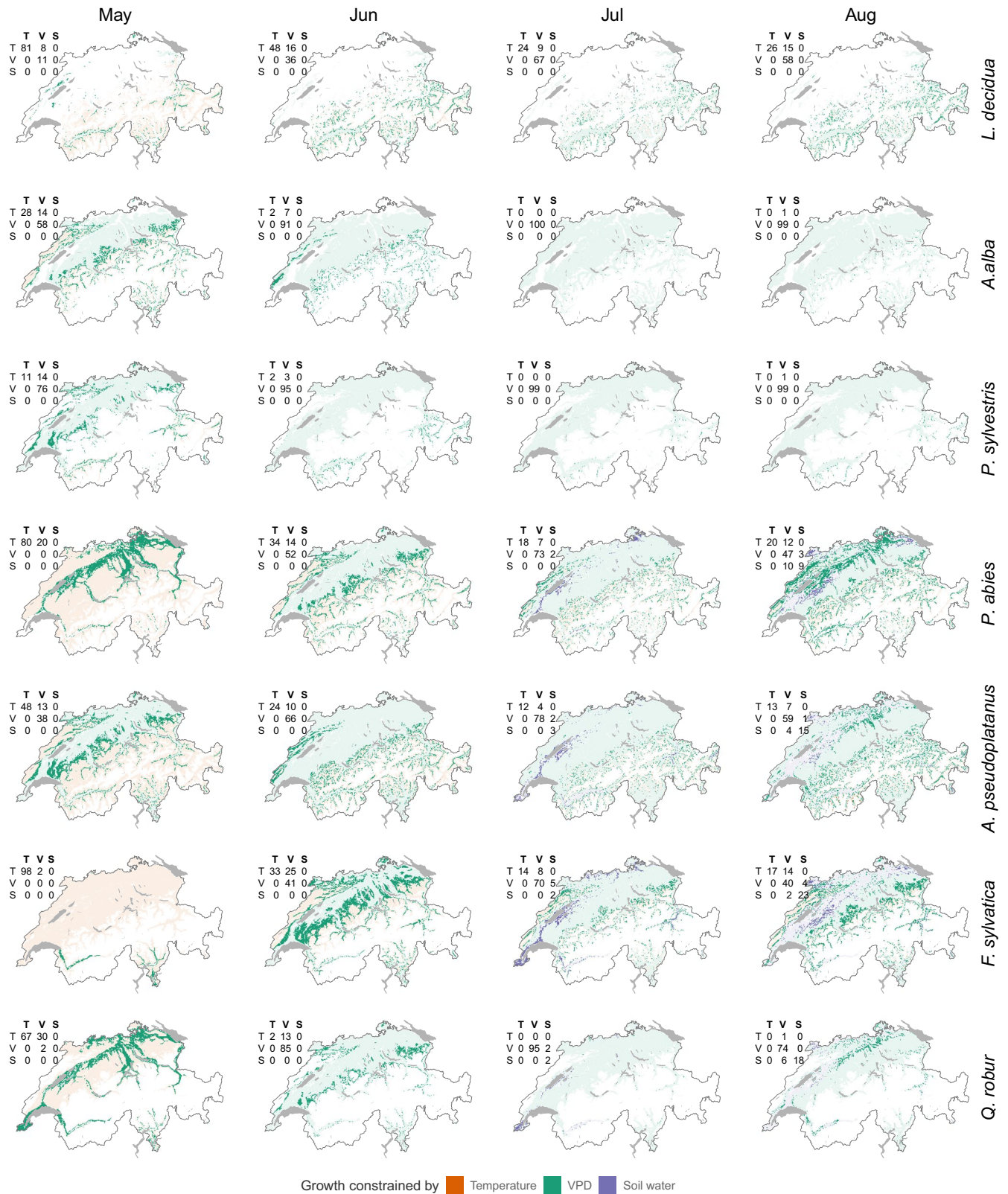
FIGURE 3 Changes in the dominant environmental constraints for each species in the 1991–2018 period relative to 1961–1990. The spatial location of environmental constraints that changed are indicated by solid colours, whereas those that remained unchanged are indicated by shaded colours. Tables indicate the transition matrix in percent of dominant environmental constraint from 1961–1990 (left) to 1991–2018 (top; T – Temperature, V – VPD, S – Soil water). Diagonals of the matrices show the proportion of grid cells without change

on the growth of seven widespread European tree species along large environmental gradients. This novel approach further allowed us to evaluate the relative importance of VPD, temperature and soil water availability as constraints on forest growth. We found that VPD was a key limiting factor for all species in the mid elevational range (700–1,200 m a.s.l.) over the entire study period (1961 to 2018), but not for the lower and upper elevations. Over the same period, forest growth at higher elevation (above 1,200 m a.s.l.) and at the beginning of the growing season was mainly constrained by low temperatures. Our results further indicate a shift in environmental constraints from low temperatures to high VPD limitation over the last 30 years, suggesting that VPD is becoming a more important factor under climate change.

Our study highlights that VPD has been a primary environmental constraint on forest growth since the early 1960s. Yet, whereas much of the recent research has been oriented towards forest responses to increasing temperatures (Allen et al., 2010), reduced precipitation (Way & Oren, 2010) and rising CO_2 (Higgins & Scheiter, 2012), growth response to VPD is still less explored although highly relevant (Gharun et al., 2020; Grossiord et al., 2020). Our findings confirm theoretical developments and recent empirical and modelling efforts, suggesting that the impact of VPD on forest functioning may be more substantial than previously assumed. In addition to being acknowledged as a primary driver and accelerator of large-scale tree mortality (Breshears et al., 2013; Williams et al., 2013) and for being positively correlated with wildfires (Seager et al., 2015; Williams et al., 2014), periods of high VPD have been identified as an essential limitation to tree growth (Babst et al., 2019; Restaino et al., 2016; Williams et al., 2013). This VPD impact, however, is not independent from other environmental constraints. During extreme years, soil water availability can become a dominant limiting factor, and its effect is exacerbated by increasing VPD, leading soil water depletion. The underlying physiological processes driving changes in forest growth are likely associated with the reduction or even temporary cessation of photosynthesis under high VPD due to CO_2 diffusional limitations (i.e. closed stomata), impaired phloem transport that concurrently limits the supply of carbon to sink tissues, and xylem cavitation caused by water tension above critical thresholds within the xylem (i.e. associated with reduced soil water supply and induced by residual transpiration through cuticles and incompletely closed stomata) during periods of high VPD (Cochard, 2019; Duursma et al., 2019; Grossiord et al., 2020; Pappas et al., 2020). To further verify our findings, it will be interesting to compare the current results of 3-PG simulated environmental growth constraints with simulations from a more explicit photosynthesis model that directly accounts for the effects of stomatal conductance on growth.

Our study shows that many of the transitions in environmental constraints on tree growth over the study period have occurred at the beginning of the growing season at lower elevations. This finding is consistent with Babst et al. (2019) who found that trees become more limited by reduced precipitation early in the growing season in hot-dry areas globally. By contrast, at the end of the growing season,

significant changes in limiting factors occurred at higher elevations. Such a change mainly corresponds to prolonged warmer summers and the resulting soil drying. Such soil drying might prevent trees from fully harnessing the benefits of a prolonged growing season and consequently limits the capacity for carbon uptake and storage (Zani et al., 2020).

We uncovered substantial variation in environmental constraints throughout the growing season and among species. For some species such as *Q. robur*, *P. abies* and *A. alba*, growth became more limited by high VPD and reduced soil water availability at lower elevations due to warmer and drier springs over the last 30 years. Morover, *P. abies*, *F. sylvatica* and *L. decidua* became more limited by VPD during longer, warmer and drier summers, mainly at higher elevations (above 1,200 m a.s.l.). These findings suggest that although VPD is increasingly affecting tree growth in most species, the impact of rising VPD may affect different growth periods depending on the species. Early in the season, high VPD and soil moisture limitations at low elevations can damage the new foliage and decrease carbon assimilation, which strongly limits current year's productivity (D'Orangeville et al., 2018). Later in the summer, long periods of high VPD and drought could subject trees to hydraulic constraints, terminate xylogenesis prematurely and limit growth and recovery strategies in subsequent years (Anderegg et al., 2015). These findings further suggest that at high elevations, we may observe a shift from warming-induced growth enhancement towards VPD- and drought-induced growth reduction (Gharun et al., 2020).

The nonlinear response of forest growth to environmental constraints implies difficulties for predictions of forest responses under future climate variability and clear limitations for space-for-time substitution approaches (Klesse et al., 2020; Wilmking et al., 2020). Previous research on trade-offs between growth constraints has demonstrated an increased sensitivity towards water demand in recent years (Babst et al., 2019; Schurman et al., 2019). A similar reduction in temperature limitations and increased limitations by VPD was found in our study, especially at lower elevations. Thus, a better understanding of the impacts of rising VPD and global warming on species-specific forest growth is urgently needed, particularly as they are climatic variables that we can project with the highest confidence. Understanding the spatial and temporal variability in growth environmental constraints will help generate accurate species-specific risk maps for forest managers, which could be used to identify and prioritize hotspot areas under increasingly frequent drought and heat stress in the near future.

5 | CONCLUSIONS

We used process-based 3-PG model simulations benchmarked by a global tree-ring dataset to identify the environmental growth constraints (VPD, cold temperatures and soil water) of seven major Central European tree species across Switzerland. We have shown at a high spatial resolution that forest growth is limited in a complex

and seasonally variable way by environmental constraints, particularly during the growing season (May–August). Our simulations suggest that growth is mainly constrained by low temperatures at higher elevations, high VPD at mid- to low elevations, and available soil water at low elevations, particularly towards the end of the growing season. Importantly, there is a substantial increase in areas limited by high VPD during the recent warmer climate (1991–2018) compared to the reference period (1961–1990). This suggests that the increasing VPD as induced by global warming, will limit tree growth by replacing temperature constraints across large areas. Although uncertainty remains about the underlying mechanisms driving VPD impacts on tree functioning, we conclude that rising evaporative demand is increasingly constraining tree growth in Swiss—and therefore also in Central European—forests. If we aim to predict the consequences of a rapidly warming climate effectively, future empirical and modelling efforts should sharpen their focus on the amplifying role of VPD and its inter-dependency with temperature and available soil water.

ACKNOWLEDGEMENTS

AUTHORS' CONTRIBUTIONS

V.T., W.E., D.I.F. and N.B. designed the research; V.T. performed the analysis; V.T., F.B. and C.G., D.I.F. wrote the paper with substantial inputs from A.G., N.B., M.S. and W.E.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13712.

DATA AVAILABILITY STATEMENT

All simulations in this study were done using the open access R package R3PG (Trotsiuk, Hartig, & Forrester, 2020). The source code is publicly available via The Comprehensive R Archive Network (CRAN) https://cran.r-project.org/web/packages/r3PG/index.html. The species-specific parameters for the model were derived from previous calibrations of 3-PG done for Switzerland (Forrester et al., 2021; Trotsiuk, Hartig, Cailleret, et al., 2020). The climatic data for simulations on the Swiss scale were provided by the Landscape Dynamics group (WSL, Switzerland). The full results of simulations are available from the EnviDat repository (Trotsiuk, Babst, et al., 2020).

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