



How did Swiss forest trees respond to the hot summer 2015?

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Abstract

Central Europe experienced an exceptionally hot summer in 2015. The area of investigation in the Central Alps in Switzerland faced the second warmest summer since the beginning of measurements in 1864. As a consequence, agriculture suffered from considerable production losses. But how were forests affected by the hot summer? We analyzed stem growth data, measured by automated point dendrometers, from 50 trees across nine sites covering the four main Swiss tree species spruce (*Picea abies*), fir (*Abies alba*), beech (*Fagus sylvatica*) and oak (*Quercus spp.*) in the years 2014 (relatively wet and cool) and 2015 (hot and dry). Annual growth and environmental conditions were determined by, and related to, the growing period based on daily resolved growth data. Our multi-species approach revealed a wide range of responses. Radial growth of spruce was largely reduced during the hot summer 2015 for sites located below 1500 m a.s.l. Growth of beech responded even positively at several sites on the Swiss Plateau. Fir and oak did not significantly deviate from their respective average growth rate. We conclude that one hot summer actually matters for stem growth, but its effect is not a priori negative. The timing of the heat wave is of highest importance. A relatively wet previous year, a wet spring and the relatively late occurrence of the heat wave in the wood growth period led to a less strong growth reduction than what could have been expected from agricultural plants. Endogenous effects like mast fruiting and legacy effects from past conditions are suggested to further play an important role for stem growth.

Zusammenfassung

Mitteleuropa erlebte einen außergewöhnlich heißen Sommer im Jahr 2015. Das Untersuchungsgebiet über verschiedene Höhenstufen in den Zentralalpen der Schweiz verzeichnete den zweitwärmsten Sommer seit Beginn der Messungen im Jahr 1864. In der Folge erlitt die Landwirtschaft erhebliche Produktionsverluste. Aber wie wirkte sich der heiße Sommer auf die Wälder aus? Wir analysierten Stammwachstumsdaten der Jahre 2014 (relativ nass und kühl) und 2015 (heiß und trocken), gemessen mit automatischen Punktdendrometern an 50 Bäumen der vier wichtigsten Schweizer Baumarten Fichte (*Picea abies*), Tanne (*Abies alba*), Buche (*Fagus sylvatica*) und Eiche (*Quercus spp.*) an neun Standorten. Das Stammwachstum wurde anhand der täglich aufgelösten Daten

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über die Wachstumsperiode bestimmt und mit Umweltmessungen in Beziehung gesetzt. Die jährlichen, radialen Stammzuwächse waren art-spezifisch und sehr heterogen. Das Stammwachstum der Fichte war im heißen Sommer 2015 für Standorte unter 1500 m ü. M. stark unterdurchschnittlich. Die Buche hingegen reagierte an mehreren Standorten im Schweizer Mittelland sogar positiv. Tanne und Eiche unterschieden sich nicht signifikant von ihrer jeweiligen durchschnittlichen Wachstumsrate. Wir schließen daraus, dass ein heißer, trockener Sommer tatsächlich für das Stammwachstum wichtig ist, aber seine Wirkung nicht a priori negativ sein muss. Das Timing der Hitzewelle ist von höchster Bedeutung. Ein relativ feuchtes Vorjahr, ein feuchter Frühling und das relativ späte Auftreten der Hitzewelle in der Holzwachstumsperiode führten zu einem weniger starken Wachstumsrückgang als von landwirtschaftlichen Pflanzen erwartet werden konnte. Wir vermuten, dass zusätzlich zu den außergewöhnlichen Umweltbedingungen im Sommer 2015, sogenannte Legacy-Effekte aus früheren Jahren sowie Mastfrucht-Dynamiken eine wichtige Rolle für das Stammwachstum spielten.

Keywords dendrometer, drought stress, global warming, heat wave, tree species, stem growth

Electronic supplementary material supplementary material (*Table S1* and *Fig. S1*) available at: <http://dx.doi.org/10.12854/erde-2018-420>

1. Introduction

Central Europe experienced an exceptionally hot summer in 2015 (Ionita et al. 2017; Muthers et al. 2017). In Switzerland, it was the second warmest summer since the beginning of modern measurements in 1864 (MeteoSwiss 2016) and it was only topped by the extreme summer 2003 (MeteoSwiss 2015b). Summer air temperatures were 2.3 °C higher and precipitation amounts were regionally 60-80% lower compared to the long-term average from 1981 to 2010 (MeteoSwiss 2018). Even the hot summer 2018 did not reach the 2015 values (2.0 °C above the long-term average) and was also less dry, however, with large regional differences.

Air temperatures were high in June (fourth warmest June ever recorded), but the exceptional heat occurred in July with two pronounced heat waves in the beginning of July (1 to 7 July) and in mid July (16 to 24 July) with daytime temperatures far above 30 °C. While all three summer months were characterized by below average precipitation amounts, July was especially dry (many regions with less than 50% of the long-term average) (MeteoSwiss 2016). Summer precipitation anomalies were similar in 2003 and 2015, but in contrast to 2003, spring 2015 was relatively warm and wet (MeteoSwiss 2015a). Overall, the summer 2015 was a prime example for summers as they are projected for future climate in Switzerland, namely warmer and drier (CH2011 2011; Scherrer et al. 2016). Agricultural production was reported to be markedly reduced by this heat wave (Bundesamt für Umwelt 2016), but how did forest trees deal with this extreme event in terms of stem growth?

The physiological mechanisms underlying stem growth are still not fully understood, because growth is not solely driven by actual weather conditions but is also largely affected by conditions of the previous winter (Cook et al. 2012; Haeni et al. 2017), or even further back in time (Anderegg et al. 2015; Mullerova et al. 2016; Ogle et al. 2015; Shao et al. 2016; Thomas et al. 2009; van der Maaten-Theunissen et al. 2016; Zielis et al. 2014; Zweifel and Sterck 2018). Independent of these so-called legacy effects, which may explain more than half of the inter-annual variation of net ecosystem productivity (Haeni et al. 2017) and stem growth (Zweifel et al. 2010), there is still a considerable direct effect of current conditions on stem growth as known from many studies (Feichtinger et al. 2014; Gessler et al. 2007; Granier et al. 2007; Herrmann et al. 2016; Hinckley et al. 1979; Latte et al. 2016; Vanoni et al. 2016; Weemstra et al. 2013).

In order to study stem growth in Swiss forests during the hot summer 2015, we used data from TreeNet (www.treenet.info), a network providing continuous, high-resolution data (10 minutes) on stem growth by automated dendrometers connected to a central database via a telecommunication link. The study covered four main tree species at nine sites across Switzerland north of the Alps. Our objectives were to assess the species- and site-specific impacts of the hot and dry summer 2015 on stem growth in comparison to the cool and wet summer 2014 in Switzerland. We followed the hypotheses (i) that annual stem growth in 2015 was generally smaller than in 2014 due to reduced precipitation and increased air temperatures in summer 2015;

(ii) that the extent of annual growth reduction in 2015 was species-specific, and (iii) that growth reductions were associated with regional variations in temperature and precipitation during the stem growth period.

2. Material and methods

2.1 Sites and setup

The nine sites studied are part of TreeNet (www.treenet.info), a network in which stem growth is assessed by measuring stem radius (SR) changes of trees with high-precision point dendrometers in forests. The sites are located at different elevations ranging from low colline to subalpine forests (from 450 to 1650 m a.s.l.) in Switzerland. All forests are managed sustainably and are either deciduous, coniferous or mixed forests (Table 1). We investigated a total number of 50 individual trees from four species, including Norway spruce (*Picea abies*) and silver fir (*Abies alba*), the two most abundant coniferous tree species in Switzerland, as well as European beech (*Fagus sylvatica*), the most abundant deciduous tree species in Switzerland, and oak (pooling *Quercus robur* and *Quercus petraea*), which is known to tolerate hot and dry conditions relatively well. High precision point dendrometers (ZN11-T-WP and ZN11-T-IP, Natkon, Oetwil am See, Switzerland) measuring stem radius (SR) changes above bark at micrometer resolution were installed on the stem of each tree. Data were collected automatically with DecentLab data loggers (DecentLab GmbH,

Dübendorf, Switzerland) at all sites, except at Davos and Lägeren, where CR1000 (Campbell Scientific Ltd., Shepshed, UK) data loggers were used. Measurements (DecentLab data loggers: every 30 s, CR1000 data loggers: every 20 s) were averaged to seven minutes (DecentLab) and ten minutes (CR1000) intervals. Measurements from DecentLab data loggers were finally interpolated to standard ten-minute intervals. This work relies on dendrometer data of the years 2014 and 2015.

2.2 Environmental data

For each TreeNet site, meteorological data (air temperature and precipitation) were obtained either directly in-situ or from nearby MeteoSwiss stations (Table S1). At all sites, overall data availability during the defined growing period was > 95% for both temperature and precipitation, except for the Beatenberg site in 2015, where a gap had to be filled using data from the closest MeteoSwiss station (i.e., Interlaken). At each of the TreeNet sites, one sensor to measure soil water potential (MPS2, Decagon Devices, Pullman, USA) was installed in the topsoil about 10 cm below ground. In order to characterize the years 2014 and 2015 meteorologically, and especially the respective summer months, monthly deviations of air temperature and precipitation from the long-term average (1981 to 2010) were obtained from nearby MeteoSwiss stations (Table S1).

Table 1 Overview of geographical location and elevation as well as species composition for the nine sites investigated. Source: Metadata base of the project TreeNet

TreeNet Site	Lat (°N)	Long (°E)	Elevation (m a.s.l.)	Forest characterization	Species (number of trees)
Beatenberg (Bea)	46.70	7.76	1510	Subalpine coniferous forest	<i>Picea abies</i> (4), <i>Abies alba</i> (2)
Davos (Dav)	46.82	9.86	1650	Subalpine coniferous forest	<i>Picea abies</i> (9)
Jussy (Jus)	46.23	6.29	500	Deciduous forest	<i>Quercus robur</i> (3)
Lägeren (Lae)	47.48	8.36	694	Mixed forest	<i>Picea abies</i> (1), <i>Abies alba</i> (3), <i>Fagus sylvatica</i> (4)
Lausanne (Lau)	46.59	6.66	810	Mixed forest	<i>Picea abies</i> (2), <i>Fagus sylvatica</i> (2)
Muri (Mur)	47.27	8.36	490	Mixed forest	<i>Picea abies</i> (3), <i>Fagus sylvatica</i> (2)
Riehen (Rie)	47.59	7.68	450	Deciduous forest	<i>Fagus sylvatica</i> (3), <i>Quercus petraea</i> (2)
Vordemwald (Vor)	47.28	7.89	480	Mixed forest	<i>Picea abies</i> (2), <i>Abies alba</i> (2), <i>Fagus sylvatica</i> (2)
Wangen (Wan)	47.42	8.65	490	Mixed forest	<i>Picea abies</i> (2), <i>Fagus sylvatica</i> (2)

2.3 Calculation of annual stem growth

Raw data series of SR were pre-processed automatically with an R script running on the server structure of the TreeNet network. Data were resampled at 10-minute resolution. Outliers and data shifts were removed based on the analysis of a frequency distribution of the ten minute-step differences between two readings. Furthermore, gaps of up to two hours were linearly interpolated. Additionally, the SR data were manually checked for plausibility and cleaned from undetected errors.

The annual stem radius increment (SRI) from point dendrometer measurements was derived as the difference between the previous and current year maximum. Intra-annual stem growth (GRO) at time t was determined from the difference between SR at time t and the maximum SR measured in the past (Zweifel et al. 2016). If this difference was negative, GRO was set to zero. If this difference was positive, GRO increased. Thus, GRO refers to the stem size increment only and neglects e.g., lignification and other processes which are not affecting size but are of interest for quantifying carbon allocation (Cuny et al. 2015). In contrast to ‘growth’ referred to in dendrochronological analyses, GRO based on automated dendrometer readings includes growth of wood and bark tissues (Zweifel et al. 2016). The absolute annual increment of stem area per tree (GRO_{abs} in cm^2) was calculated from SRI and diameter at breast height (dbh, measured with a caliper):

$$GRO_{abs} = \left(\frac{dbh}{2} + SRI\right)^2 \pi - \left(\frac{dbh}{2}\right)^2 \pi \quad (1)$$

To compare annual stem growth across species and sites, we normalized GRO_{abs} by the cross-section area derived from dbh resulting in stem growth normalized by dbh (GRO_n in %):

$$GRO_n = \frac{GRO_{abs}}{\left(\frac{dbh}{2}\right)^2 \pi} \quad (2)$$

We refer to the difference in annual stem growth between 2015 and 2014 as value of 2015 minus value of 2014, thus, a negative difference reflects less stem growth in 2015 compared to 2014. In order to account for fast- and slow-growing trees, the differences in stem growth between the two years were normalized for each tree by its mean annual stem growth (mean of 2014 and 2015):

$$\Delta GRO_n = \frac{GRO_{n,2015} - GRO_{n,2014}}{GRO_{n(2014,2015)}} \quad (3)$$

2.4 Determination of stem growth periods

Tree-specific stem growth periods per tree and year were determined from the SR measurements. The start and end of the growth period (GRO_{start} , GRO_{end}) were defined as the time when 5% and 95% of SRI were reached (Fig. 1). Mean stem growth periods were calculated per site and species over the two years 2014 and 2015 as an average of the individual trees.

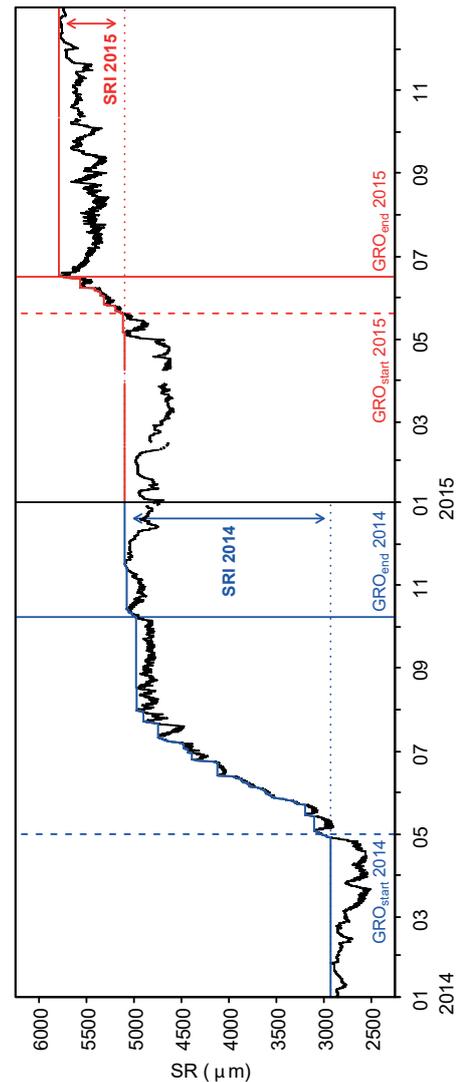


Fig. 1 Determination of annual increase in stem radius (SRI), growing period start (GRO_{start}) and end (GRO_{end}) from stem radius (SR) measurements. Black line shows the SR measurements from which step-like growth curves (blue in 2014, red in 2015) were derived, assuming zero growth during periods of stem shrinkage according to Zweifel et al. (2016). The annual SRI represents the annual sum of the growth curve and is only determinable if the maximum SR of the previous year is known. GRO_{start} and GRO_{end} of the growing period were defined as the time when 5% and 95% of SRI were reached, respectively. Source: Database of the project TreeNet

2.5 Characterization of meteorological conditions during the stem growth period

Site-specific precipitation sums and growing degree days (GDD) were calculated over the mean stem growth periods of the two years 2014 and 2015. GDD was calculated as

$$GDD = \sum (\bar{T}_{daily} - T_{base}) \quad (4)$$

where \bar{T}_{daily} is mean daily temperature, T_{base} as set to 5.56 °C as suggested by Gunderson et al. (2012) and days with $\bar{T}_{daily} < T_{base}$ were ignored.

Data processing and analyses were performed in R version 3.3.1 (R Core Team 2016).

3. Results

3.1 Meteorological conditions in spring and summer 2014 and 2015

In 2014, air temperatures during March, April and June were above the long-term average, whereas it was below the long-term average in May, July and August for all sites (Fig. 2). Precipitation showed an exceptional peak in July for all sites resulting in strong positive deviations from the long-term average for summer 2014.

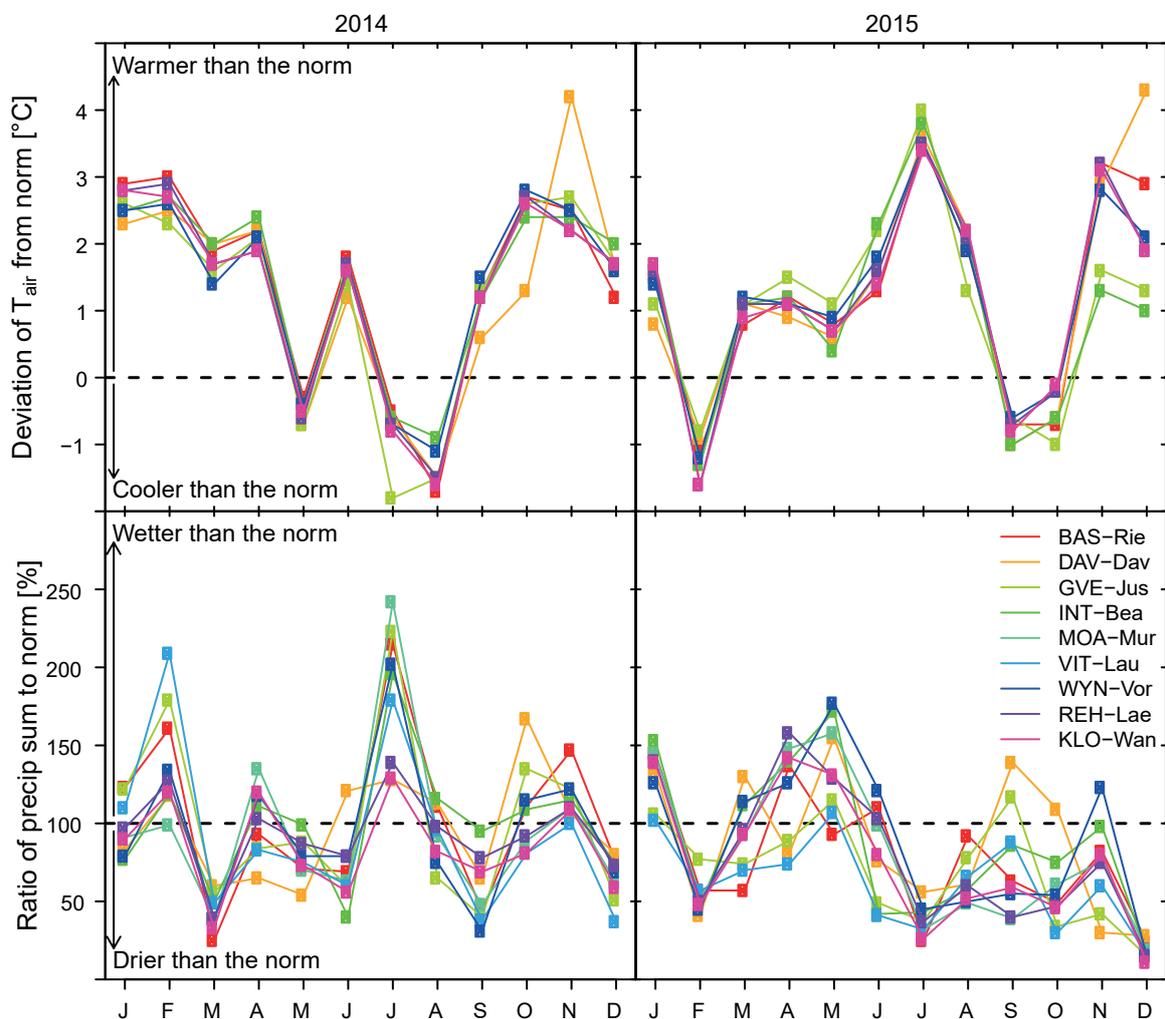


Fig. 2 Meteorological conditions during the years 2014 (left) and 2015 (right) in comparison to the long-term average (1981 to 2010). Top panels: deviation of monthly mean air temperature (T_{air} , 2m height, dashed line indicates zero deviation) from the long-term average (°C); lower panels: percentage of monthly precipitation sums (precip) to the long-term average (%; dashed line indicates zero deviation). Coloured lines represent nine MeteoSwiss stations, each of which is closest to one of the TreeNet sites. Legend shows station pairs (MeteoSwiss station – TreeNet site), for site abbreviations refer to Table S1). For the two MeteoSwiss sites Villars-Tierclin (VIT) and Mosen (MOA) no temperature deviations were available, because the time series did not cover the full period from 1981 to 2010. Data source: MeteoSwiss 2016

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The hot year 2015 was characterized by positive deviations from the long-term average of monthly mean air temperatures for the spring months March, April and May and, increasingly pronounced, for the summer months June, July and August at all sites (Fig. 2). Precipitation in March, April and May was above-average at some sites, but below the long-term average at others. However, it was clearly below the long-term average for the summer months July and August over all sites.

Spring and summer 2015 were clearly warmer than 2014, whereas spring was wetter and summer was drier in 2015 compared to 2014. Thus, in 2015, a warm and wet spring was followed by a hot and dry summer.

3.2 Annual stem growth increments

Mean absolute annual stem growth (GRO_{abs}) was generally higher for coniferous species compared to deciduous species and ranged from 11.1 to 58.2 $cm^2 yr^{-1}$ for spruce and from 34.1 to 76.1 $cm^2 yr^{-1}$ for silver fir, whereas it ranged from 3.3 to 35.6 $cm^2 yr^{-1}$ for beech and from 7.4 to 32.0 $cm^2 yr^{-1}$ for oak. Also mean annual stem growth normalized by dbh (GRO_n) was found to be species-specific and ranged from 0.5 to 5.4% for spruce, from 1.2 to 2.4% for silver fir, from 0.2 to 2.8% for beech and from 0.9 to 2.1% for oak (for more details see Table 2). Differences between GRO_{abs} and GRO_n became particularly evident for spruce, which generally showed low GRO_{abs} at Davos and Beaten-

Table 2 Mean absolute growth (GRO_{abs}) (\pm standard deviation) and growth normalized for stem diameter at breast height (dbh) (GRO_n) for the years 2014 and 2015 and the respective differences between the years 2014 and 2015 for Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and oak (*Quercus robur* and *Quercus petraea*). Source: Database of the project TreeNet

Site	Species	n	Absolute growth (GRO_{abs} , $cm^2 yr^{-1}$)					Normalized growth (GRO_n , %)						
			2014		2015		2015 - 2014	2014		2015		2015 - 2014		
Beatenberg (Bea)	<i>Abies alba</i>	2	39.1	± 47.4	34.2	± 38.9	-5.0	± 8.5	1.3	± 1.3	1.2	± 1.1	-0.1	± 0.3
	<i>Picea abies</i>	4	20.9	± 6.2	22.0	± 6.5	1.1	± 2.4	2.0	± 1.7	2.2	± 1.7	0.1	± 0.2
Davos (Dav)	<i>Picea abies</i>	9	20.6	± 10.6	19.8	± 11.1	-0.8	± 4.8	1.8	± 0.5	1.5	± 0.5	-0.2	± 0.5
Jussy (Jus)	<i>Quercus robur</i>	3	8.6	± 4.4	7.4	± 2.2	-1.2	± 2.2	1.1	± 0.3	1.0	± 0.1	-0.1	± 0.2
Lägeren (Lae)	<i>Abies alba</i>	3	65.5	± 53.9	76.1	± 66.1	10.6	± 15.1	1.6	± 0.6	2.0	± 0.9	0.4	± 0.3
	<i>Fagus sylvatica</i>	4	33.0	± 13.2	35.6	± 15.5	2.6	± 15.5	2.8	± 1.8	2.5	± 1.4	-0.3	± 0.7
	<i>Picea abies</i>	1	21.3		11.1		-10.3		5.4		2.8		-2.6	
Lausanne (Lau)	<i>Fagus sylvatica</i>	2	34.7	± 2.4	32.3	± 2.1	-2.4	± 4.5	0.8	± 0.2	0.8	± 0.1	-0.1	± 0.1
	<i>Picea abies</i>	2	58.2	± 51.3	38.1	± 39.8	-20.1	± 11.5	0.8	± 0.5	0.5	± 0.4	-0.3	± 0.1
Muri (Mur)	<i>Fagus sylvatica</i>	2	3.3	± 0.9	6.8	± 2.3	3.4	± 3.2	0.2	± 0.1	0.4	± 0.0	0.2	± 0.1
	<i>Picea abies</i>	3	32.1	± 23.6	14.4	± 6.6	-17.7	± 17.8	1.8	± 0.6	0.9	± 0.2	-0.9	± 0.5
Riehen (Rie)	<i>Fagus sylvatica</i>	3	31.1	± 20.3	29.9	± 15.1	-1.2	± 7.1	1.4	± 1.0	1.3	± 0.7	-0.1	± 0.3
	<i>Quercus petraea</i>	2	32.0	± 2.5	29.3	± 4.9	-2.7	± 7.4	1.0	± 0.3	0.9	± 0.0	-0.1	± 0.3
Vordemwald (Vor)	<i>Abies alba</i>	2	47.4	± 25.0	35.4	± 0.1	-12.0	± 25.0	2.4	± 0.4	2.1	± 1.4	-0.2	± 1.0
	<i>Fagus sylvatica</i>	2	5.9	± 4.7	6.6	± 5.5	0.7	± 0.9	1.4	± 1.2	1.6	± 1.4	0.2	± 0.2
	<i>Picea abies</i>	2	43.2	± 19.7	14.9	± 7.9	-28.3	± 11.8	2.8	± 1.0	1.0	± 0.4	-1.8	± 0.6
Wangen (Wan)	<i>Fagus sylvatica</i>	2	14.2	± 8.2	17.9	± 7.2	3.7	± 1.0	1.2	0.9	1.5	± 0.9	0.3	± 0.0

berg (sites with relatively low dbh and at high elevation) and high GRO_{abs} at Lausanne (large dbh) while this pattern was reversed for GRO_n (Fig. 3). In order to

compare annual stem growth between sites and species, and across the two years we focused on GRO_n in the further analyses.

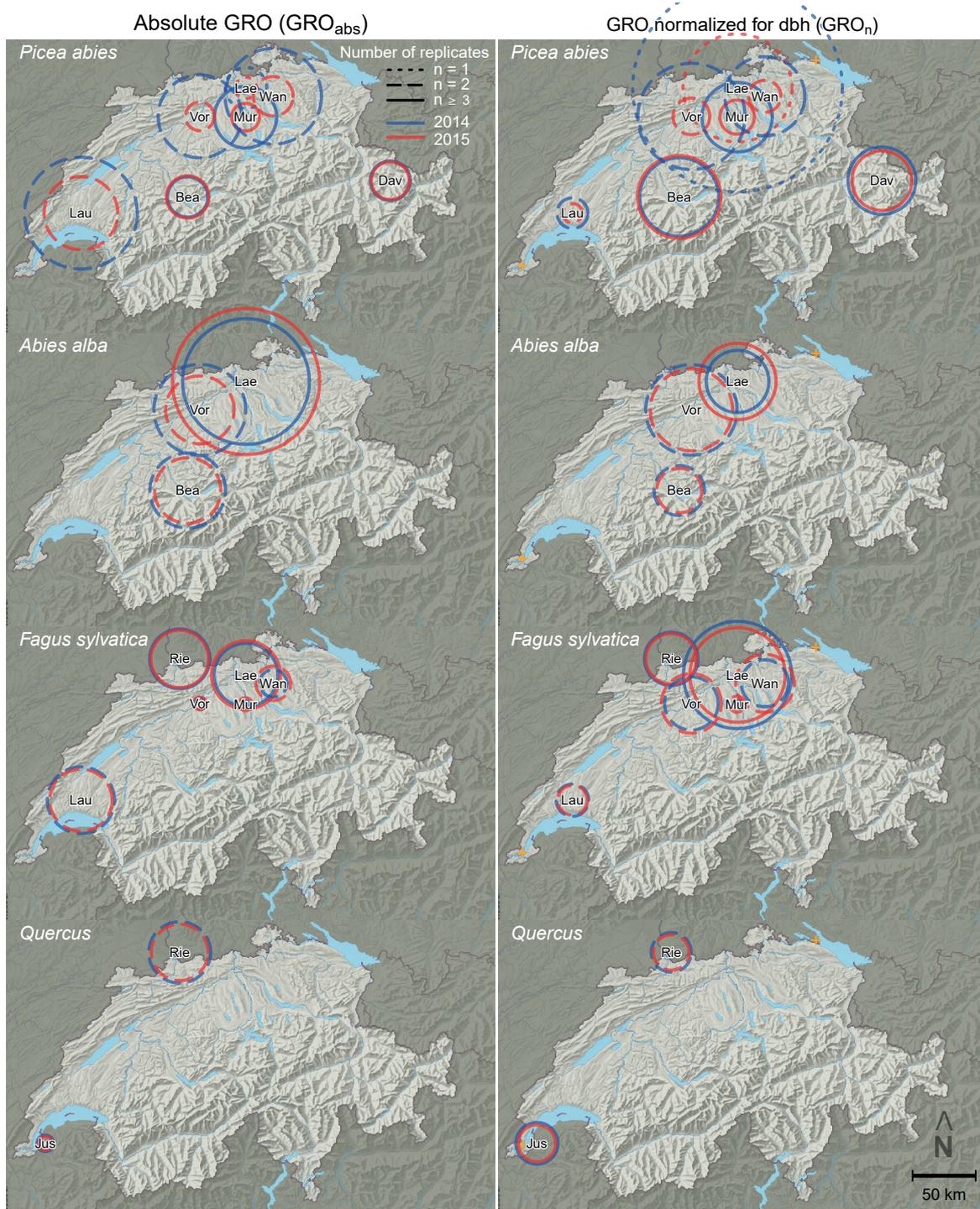


Fig. 3 Maps of Switzerland with the annual tree growth per site, species and year. Mean absolute stem growth (left panels, GRO_{abs}) and mean stem growth normalized for diameter at breast height (dbh) (right panels, GRO_n) are shown for Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and oak (*Quercus* including *Quercus robur* and *Quercus petraea*) for the years 2014 (blue) and 2015 (red). Circle size depicts annual growth and is comparable across species. GRO_{abs} and GRO_n ranged from 3.3 to 76 $cm^2 yr^{-1}$ and 0.2 to 5.4%, respectively. Line type illustrates replication per site (solid: $n \geq 3$, dashed: $n = 2$, dotted: $n = 1$). For site abbreviations refer to Table 1. Source: Database of the project TreeNet

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We observed lower GRO_n in 2015 compared to 2014 at several sites, particularly for spruce, but with large site- and species-specific variations (Fig. 4). Differences between GRO_n of the two years (ΔGRO_n) revealed that spruce consistently grew less in 2015 compared to 2014 except at Beatenberg, a high-elevation site. Generally, ΔGRO_n of spruce trees was smaller at sites located at higher elevations (> 1500 m a.s.l., i.e., Beatenberg and Davos) than at sites located at lower elevations ($R^2 = 0.89$; $p < 0.05$).

For silver fir, ΔGRO_n was smaller compared to spruce and less clear patterns appeared, possibly also because data of fewer sites were available. Also for oak, ΔGRO_n was small, with two sites showing almost the same growth in both years. Beech, on the other hand, grew on average slightly better in 2015 compared to 2014 at all sites except at Lausanne, however, with large variations observed in ΔGRO_n across- and within-sites (Fig. 4).

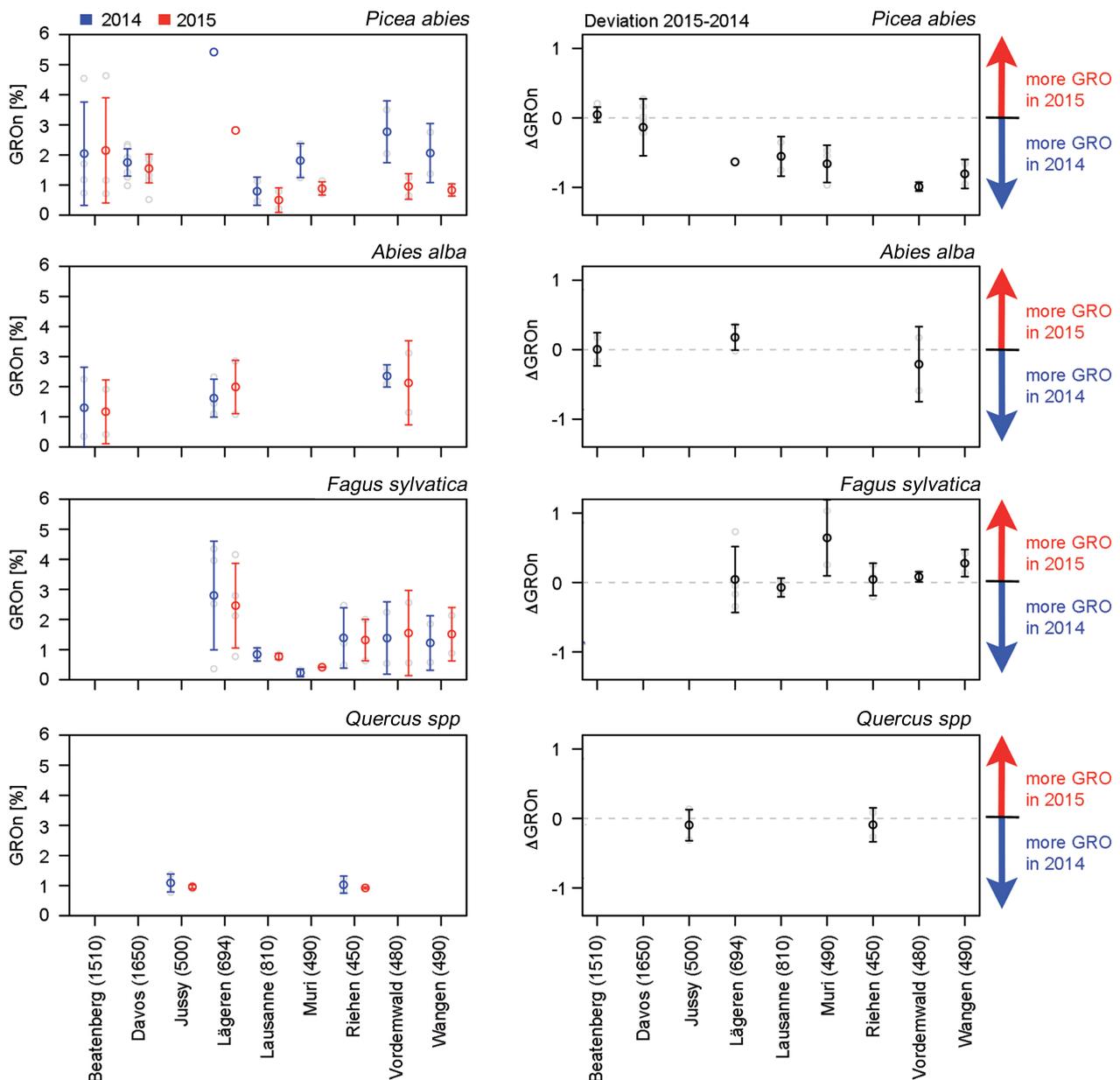


Fig. 4 Site-specific mean annual stem growth normalized for diameter at breast height dbh (left panels, GRO_n) for the years 2014 (blue) and 2015 (red). Normalized deviations between the two years (ΔGRO_n) are shown in the right panels. Results were calculated for Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and oak (*Quercus robur* and *Quercus petraea*). Error bars show the standard deviation, the number in brackets behind site name indicates the site elevation (m a.s.l.). Source: Database of the project TreeNet

3.3 Patterns of stem growth periods

We observed large variations in start (GRO_{start}), end (GRO_{end}) and total length of the stem growth period (GRO_{length}) of individual trees for the different species, sites, and years (Fig. 5). GRO_{start} of spruce and silver fir significantly depended on elevation, with sites located at higher elevations starting their growing periods later (spruce: $R^2 = 0.61-0.77$, $p < 0.001$, +3 days per 100 m additional elevation; silver fir: $R^2 = 0.82-0.85$, $p < 0.01$, 3–4 days per 100 m). We found no significant relationships between GRO_n and GRO_{start} , GRO_{end}

or GRO_{length} for any of the species or any of the years. Despite increased precipitation deficits and air temperatures during summer 2015, we did not find a consistently earlier ending of the growing period in 2015. Only some of the trees had an earlier GRO_{end} in 2015 compared to 2014 (spruce: 9 out of 23, silver fir: 3 out of 7 trees, beech: 10 out of 15, oak 3 out of 6). However, all trees with one exception stopped growing earlier in 2015 compared to 2014 at Wangen and Riehen. Spruce tended to grow over a longer period but less in size in 2015, while beech grew over a shorter period but more in size in 2015 compared to 2014.

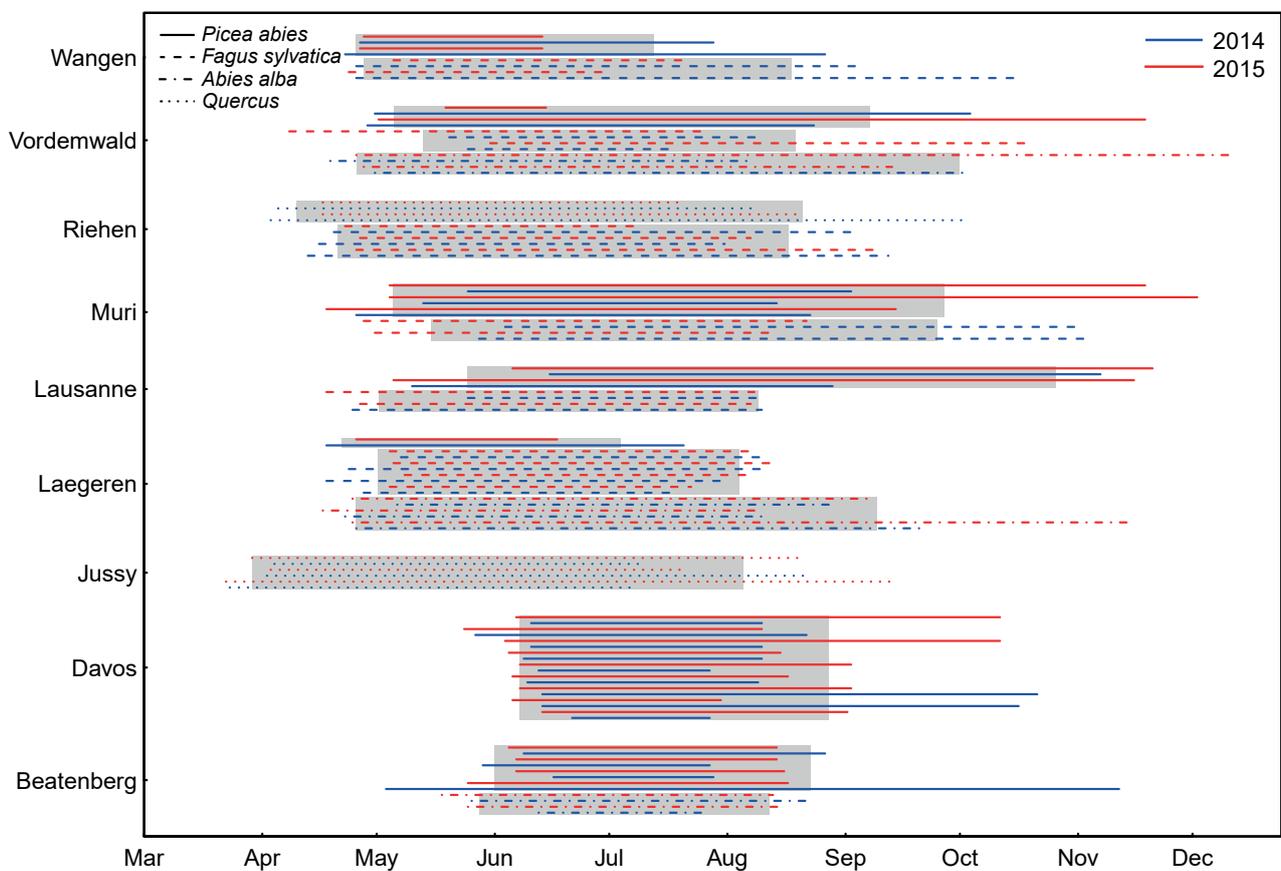


Fig. 5 Tree-specific stem growth periods for Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and oak (*Quercus* including *Quercus robur* and *Quercus petraea*) for 2014 (blue) and 2015 (red). The start and end of the growing period were defined as the time when 5% and 95% of the annual stem radial increment (SRI) were reached, respectively. Line types show different species, grey areas indicate site- and species-specific mean growing periods. Source: Database of the project TreeNet

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3.4 Stem growth in relation to air temperature and precipitation

In order to test our assumptions about the relationship between stem growth, temperature and precipitation we analyzed growing degree days (GDD) and precipitation sums during the respective site- and species-specific mean growing periods. GDD and precipitation sums during the growing period ranged from 458 to 1869 °C and from 209 to 769 mm, respectively (Fig. 6). GDD during the growing period in 2015 was consist-

ently higher compared to 2014. Precipitation sums of the growing period were generally lower in 2015 compared to 2014. While for some sites and species the difference in precipitation between 2015 and 2014 was very large (e.g. for spruce at Beatenberg), it was rather low for others (e.g. for beech at Wangen). The earlier the growth period in 2015 started the more precipitation the trees received during their growth period due to the high precipitation in spring 2015 (Fig. 2).

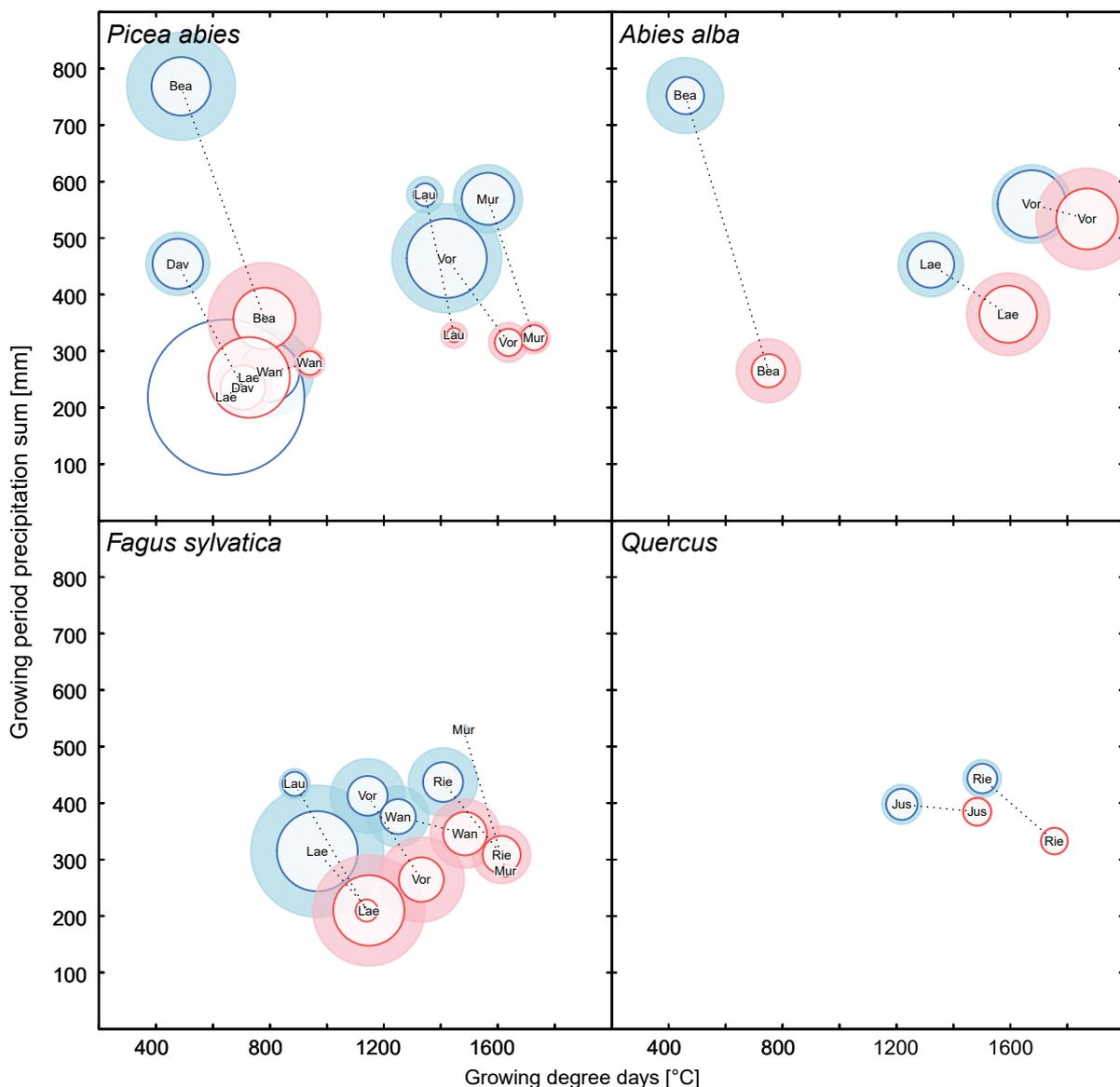


Fig. 6 Mean annual stem growth (symbol size) in relation to growing degree day (GDD) and precipitation. Mean annual stem growth was normalized for diameter at breast height (dbh) (GRO_n) for Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and oak (*Quercus* including *Quercus robur* and *Quercus petraea*) and put in relation to growing GDD and precipitation sums during the site- and species-specific mean growing periods of the years 2014 (blue) and 2015 (red). Symbol size of GRO_n is comparable across the four panels. Light blue and light red shading around the white symbols illustrate standard deviation of GRO_n . Dotted grey lines link data of the same sites of 2014 and 2015. For site abbreviations refer to Table 1. Source: Database of the project TreeNet

Despite the regional differences in meteorological conditions, we did not detect statistically significant relationships between regional differences in GRO_n and the differences in precipitation or temperature during the growing period for any species. Beech at Wangen and Muri grew better in 2015 compared to 2014 which is in line with a relatively low difference in precipitation between 2015 and 2014 (Wangen, *Fig. 6*) and with relatively high precipitation sums compared to the other sites (Muri, *Fig. 6*). The inconsistent growth pattern for beech could partly be related to general environmental conditions (*Fig. S1*). Those trees, which grew better in 2015, tended to be at sites characterized by warmer and wetter conditions during the growing period 2015, whereas those trees, which grew less in 2015, were located at sites characterized by cooler and drier conditions during the growing period 2015. However, there were also exceptions to this observation (such as one tree at Riehen and some trees at Lägeren and Lausanne).

Moreover, the two sites showing consistently higher annual beech growth in 2015 compared to 2014 (Muri and Wangen) were characterized by less water deficit in the topsoil during summer 2015 compared to 2014 (less negative SWP, *Fig. S1*). With increasing soil drought, the soil water potential pattern became less consistent in its effect on tree growth with some trees still growing better in 2015 compared to 2014, while others grew less irrespective of the measured topsoil SWP at the sites.

4. Discussion

We followed the hypotheses (i) that annual stem growth in 2015 is generally smaller than in 2014 due to reduced precipitation and increased air temperatures in summer 2015; (ii) that the extent of annual growth reduction in 2015 was species-specific, and (iii) that growth reductions were associated with regional variations in temperature and precipitation during the stem growth period.

4.1 Does one hot summer matter for annual stem growth?

As hypothesized, annual stem growth was reduced at most sites in 2015 compared to 2014 (*Table 2*), and our results confirm the well-known effect that a single extreme event, in our case one hot summer, matters for

annual stem growth (Feichtinger et al. 2014; Hinckley et al. 1979; Vanoni et al. 2016; Weemstra et al. 2013). However, in accordance with our second hypothesis, the extent of the annual growth reduction was site- and species-dependent and there were even sites and species for which average annual growth was higher in 2015 compared to 2014 (*Figs. 3 and 4*). Generally, the effect of the heat in summer 2015 on stem growth was less pronounced than expected, mainly due to the late start of the heat wave (starting in the beginning of July). Contrary to our third hypothesis, we could not significantly associate regional growth reductions with the respective variations in temperature and precipitation during the stem growth period for none of the species investigated. In the following, we discuss potential mechanisms leading to this wide range of responses.

4.2 Role of elevation

Growth and survival of trees at higher elevations are known to be temperature-limited while the soil water availability is less relevant at many sites (Körner 2012). Our findings for spruce support this view. Spruce was the species most sensitively responding to the hot summer 2015 at low elevations (*Figs. 3 and 6*). This was found to be in contrast to the high-elevation sites where spruce was hardly affected (Davos) or even grew better in 2015 (Beatenberg). Similar findings were reported from the extremely hot summer 2003 (Jolly et al. 2005) when vegetation growth was enhanced at high elevations and reduced at low elevations. Another study, partly conducted at the same sites as our study, also found increased stem growth at Beatenberg in 2003 (Pannatier et al. 2012) as we show here for 2015. Furthermore, modelling approaches project spruce to vanish from lowland sites in Switzerland with ongoing temperature increase (Bugmann et al. 2014). Our results support these projections, since spruce clearly suffered most from the hot summer in 2015 at the lowland sites, and these extreme summers are expected to become more frequent in the future (Scherrer et al. 2016).

4.3 Timing of the heat wave

Stem growth of the investigated species began in April in the year 2015 (except for the high elevation sites Davos and Beatenberg), about two months before the heat started (*Fig. 2*). With the wet and warm

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spring in 2015, the growing conditions might have been even better than in other years (*Bundesamt für Umwelt* 2016) and thus, the spring conditions are concluded to be the main reason for most tree species being affected in a relatively moderate way. This observation underlines the manifold reported importance of a wet spring for good wood growth during the following summer months (*Braun et al.* 2017; *Wolf et al.* 2016) and thus the timing of heat and drought for tree growth in general. The heat wave began too late to cause large stem growth reductions, and from this point of view the summer was not severely dry for most forest trees (*Dietrich et al.* 2018). The same weather constellation a month or two earlier would most likely have had a much stronger impact on forest trees. Most likely, the exceptionally dry summer 2018 (which was, however, not as warm as 2015) will allow additional insights in future studies to critically test our interpretation.

The only species showing a distinct growth reduction in 2015 was spruce at lower elevation sites. Its growth period did not start later than the one of the other species (*Fig. 5*), and thus the timing of the growing period does not serve as a potential explanation for the decreased growth. In a meta-analysis of *Etzold and Zweifel* (2018) including the years from 2012 to 2014 (low elevation sites only), we found that the relative contribution of the months from July onwards to annual growth was for oak (26%) significantly lower than for spruce (44%), fir (50%) and beech (43%), i.e., 74% of annual growth of oak happened until the end of June before the heat wave started. Hence, spruce should have been affected in the same way as beech and fir by the heat wave starting in July 2015. This finding does therefore not explain the bad performance of spruce. However, the growth reduction of spruce from July onwards was much larger (-37%) than for the other species (fir: -16%, beech: -16%, oak: -7%), indicating a greater heat (and drought) sensitivity of spruce. The bad growth performance of spruce is therefore most likely the result of a generally high sensitivity to high temperatures and little dependent on the timing of the heat wave.

Beech, in contrast to spruce, was found to respond unexpectedly positively to the hot summer 2015. Those individuals with higher annual stem growth in 2015 compared to 2014, tended to be located at sites that received more precipitation or had less water deficit in the topsoil during the growing period 2015 (*Fig. S1*). Thus, we suggest that beech at sites with

high soil water availability is hardly affected or may even benefit from hot summer conditions, whereas beech trees at dry sites reduce growth (see also (*Bayrische Landesanstalt für Wald und Forstwirtschaft* 2016; *Hartl-Meier et al.* 2014; *Hentschel et al.* 2016; *Pretzsch et al.* 2018)). For beech (and oak) the timing of the heat wave has played an important role, since the beech sites might have strongly benefitted from the remaining soil water from the wet spring. This is also in line with the results of *Heinrich et al.* (2018) who suggested beech to be more water- than temperature-limited. Furthermore, *Scharnweber et al.* (2011) found growth of beech to be strongly dependent on water availability during summer. These earlier studies underline the importance of the wet months early in the growing season to understand the measured stem growth responses in the dry and hot summer 2015.

4.4 Potential effects of mast fruiting

Mast fruiting is known to appear in more or less regular time steps (*Greene and Johnson* 1994; *Nussbaumer et al.* 2016). In the mass- and energy balance of a tree, a mast fruiting year requires a substantial effort, which is most likely affecting the regular energy and carbon sink in a tree, i.e., new conducting wood, phloem tissue, leaves, branches, and roots (*Greene and Johnson* 1994; *Sterck and Schieving* 2011). This leads to reduced stem growth in the mast year but possibly also in the following year. Fructification for beech in Switzerland was high in 2014 but low in 2015 and has been shown to explain about 10% of the growth variation (*Braun et al.* 2017). Thus, our work compares the relatively cool and wet mast fruiting year 2014 with the following dry year 2015. This sequence of two exceptional years for beech most likely masked the potential drought effect in 2015 because the stem growth of the year 2014 might have already been limited due to the mast and did not reach its potential growth maximum under the given environmental conditions.

4.5 Legacy effects

Another important aspect are the so-called legacy effects, because the current year stem growth is known to be significantly affected by meteorological conditions of the previous year(s) (*Ogle et al.* 2015). Buds built in autumn of the past season, and structures and resources maintained over several years (i.e., leaves,

sapwood, carbon reserves) are potentially carrying past conditions to the present, strongly determining the current year's physiology including growth (Zweifel and Sterck 2018). The longer functional structures of a tree remain active, the longer are their respective organ lifetimes and the more ancient conditions may affect the physiological response of a tree to the current environmental conditions (Zweifel and Sterck 2018). As an example, the sapwood of most tree species remains active for several years. This means that a small tree ring with low hydraulic conductance built e.g. in a drought-stress year, affects the overall hydraulic conductance of a tree over several years until it is completely replaced. During this time, the physiological performance of a tree is (slightly) lowered by this small tree ring originating from unfavourable conditions in the past. This idea of a legacy-effect on the current-years performance of a tree was recently tested with a conceptual growth model including the lifetimes of organs and reserves as variables to quantify the effect of historic conditions on current physiological (growth) responses (Zweifel and Sterck 2018). The modelling results strongly support the effect of historic conditions on the current performance of a tree. The authors of the study concluded that tree species with long lifetimes of organs and reserves are better buffered against exceptional environmental conditions, however they are also slower in positively responding to good growing conditions

Recent empirical work further supports the importance of legacy effects on stem growth (Thomas et al. 2009; Babst et al. 2012; Zielis et al. 2014; van der Maaten-Theunissen et al. 2016) and net ecosystem productivity (Cook et al. 2012; Haeni et al. 2017). Moreover, it has been shown (Shao et al. 2016) that climatic variables can only partly explain inter-annual variability in physiological parameters, and according to Vanoni et al. (2016) and Jucker et al. (2017) abrupt growth decreases in response to drought may be lagged by more than one year. Investigating such lagged responses was, however, beyond the scope of this study and would need longer time series for a sound analysis.

5. Conclusions

Our work clearly showed that trees did respond to the dry and hot summer 2015 – but not necessarily in a negative way. We observed trees growing less due to the hot and dry conditions, particularly spruce at

lower elevations. However, oak and silver fir were less affected and beech could even partly benefit from the hot summer 2015. The relatively moderate effect on these forest tree species was mainly explained by the wet and warm spring months covering about the first half of the stem growth period. Legacy effects and a beech mast year the year before the heat summer are concluded to further blur the direct impact of the heat wave on stem growth. The hot and dry summer 2018 started earlier than the one in 2015, so that future studies may particularly analyse the different tree responses in the two years to gain further insights into drought effects on forest trees.

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References

- Anderegg, W.R., C. Schwalm, F. Biondi, J.J. Camarero, G. Koch, M. Litvak, K. Ogle, J. D. Shaw, E. Shevliakova, A.P. Williams, A. Wolf, E. Ziacco and S. Pacala 2015: Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. – *Science* **349** (6247): 528-532, doi:10.1126/science.aab1833
- Babst, F., M. Carrer, B. Poulter, C. Urbinati, B. Neuwirth and D. Frank 2012: 500 years of regional forest growth variability and links to climatic extreme events in Europe. – *Environmental Research Letters* **7** (4): 1-11, doi:10.1088/1748-9326/7/4/045705
- Bayerische Landesanstalt für Wald und Forstwirtschaft 2016: Trockensommer 2015. – Weihenstephan
- Braun, S., C. Schindler and B. Rihm 2017: Growth trends of beech and Norway spruce in Switzerland: The role of nitrogen deposition, ozone, mineral nutrition and climate. – *Science of the Total Environment* **599**: 637-646, doi:10.1016/j.scitotenv.2017.04.230
- Bugmann, H., P. Brang, C. Elkin, P. Henne, O. Jakob, M. Lévesque, H. Lischke, A. Psomas, A. Rigling, B. Wermerlinger and N.E. Zimmermann 2014: Climate change impacts on tree species, forest properties and ecosystem services.

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- In: CH2014-Impacts, Toward Quantitative Scenarios of Climate Change Impacts in Switzerland, edited by F. OCCR, MeteoSwiss, C2SM, Agroscope, ProcClim. – Bern: 136
- Bundesamt für Umwelt 2016: Hitze und Trockenheit im Sommer 2015. Auswirkungen auf Mensch und Umwelt. – Bern
- CH2011 2011: Swiss Climate Change Scenarios CH2011. C2SM, MeteoSwiss, ETH, NCCR Climate, and OcCC. – Zürich
- Cook, B.I., E.M. Wolkovich and C. Parmesan 2012: Divergent responses to spring and winter warming drive community level flowering trends. – Proceedings of the National Academy of Sciences of the United States of America **109** (23): 9000-9005, doi:10.1073/pnas.1118364109
- Cuny, H.E., C.B. Rathgeber, D. Frank, P. Fonti, H. Makinen, P. Prislan, S. Rossi, E.M. del Castillo, F. Campelo, H. Vavrcik, J.J. Camarero, M.V. Bryukhanova, T. Jyske, J. Gricar, V. Gryc, M. De Luis, J. Vieira, K. Cufar, A.V. Kirdyanov, W. Oberhuber, V. Tremli, J.-G. Huang, X. Li, I. Swidrak, A. Deslauriers, E. Liang, P. Nojd, A. Gruber, C. Nabais, H. Morin, C. Krause, G. King and M. Fournier 2015: Woody biomass production lags stem-girth increase by over one month in coniferous forests. – Nature Plants **1** (11): 1-6, doi:10.1038/nplants.2015.160
- Dietrich, L., S. Delzon, G. Hoch and A. Kamen 2018: No role for xylem embolism or carbohydrate shortage in temperate trees during the severe 2015 drought. – Journal of Ecology **107** (1): 334-349
- Etzold, S. and R. Zweifel 2018: TreeNet-Daten und Analysen der ersten fünf Messjahre mit Beiträgen von Matthias Haeni, Susanne Burri, Sabine Braun, Lorenz Walthert, Melissa Dawes, Nina Buchmann, Elena Haeler, Roger Köchli, Marcus Schaub und Werner Eugster. WSL Bericht 72. WSL Birmensdorf. – Birmensdorf
- Feichtinger, L.M., B. Eilmann, N. Buchmann and A. Rigling 2014: Growth adjustments of conifers to drought and to century-long irrigation. – Forest Ecology and Management **334**: 96-105, doi:10.1016/j.foreco.2014.08.008
- Gessler, A., C. Keitel, J. Kreuzwieser, R. Matyssek, W. Seiler and H. Rennenberg 2007: Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. – Trees-Structure and Function **21** (1): 1-11, doi:10.1007/s00468-006-0107-x
- Granier, A., M. Reichstein, N. Breda, I.A. Janssens, E. Falge, P. Ciais, T. Grunwald, M. Aubinet, P. Berbigier, C. Bernhofer, N. Buchmann, O. Facini, G. Grassi, B. Heinesch, H. Ilvesniemi, P. Keronen, A. Knohl, B. Kostner, F. Lagergren, A. Lindroth, B. Longdoz, D. Loustau, J. Mateus, L. Montagnani, C. Nys, E. Moors, D. Papale, M. Peiffer, K. Pilegaard, G. Pita, J. Pumpanen, S. Rambal, C. Rebmann, A. Rodrigues, G. Seufert, J. Tenhunen, I. Vesala and Q. Wang 2007: Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. – Agricultural and Forest Meteorology **143** (1-2): 123-145
- Greene, D.F. and E.A. Johnson 1994: Estimating the mean annual seed production of trees. – Ecology **75** (3): 642-647, doi:10.2307/1941722
- Gunderson, C.A., N.T. Edwards, A.V. Walker, K.H. O'Hara, C.M. Campion and P.J. Hanson 2012: Forest phenology and a warmer climate – growing season extension in relation to climatic provenance. – Global Change Biology **18** (6): 2008-2025, doi:10.1111/j.1365-2486.2011.02632.x
- Haeni, M., R. Zweifel, W. Eugster, A. Gessler, S. Zielis, C. Bernhofer, A. Carrara, T. Grunwald, K. Havrankova, B. Heinesch, M. Herbst, A. Ibrom, A. Knohl, F. Lagergren, B.E. Law, M. Marek, G. Matteucci, J.H. McCaughey, S. Minerbi, L. Montagnani, E. Moors, J. Olejnik, M. Pavelka, K. Pilegaard, G. Pita, A. Rodrigues, M.J. Sanchez, M.J. Schelhaas, M. Urbaniak, R. Valentini, A. Varlagin, T. Vesala, C. Vincke, J. Wu and N. Buchmann 2017: Winter respiratory C losses provide explanatory power for net ecosystem productivity. – Journal of Geophysical Research-Biogeosciences **122** (1): 243-260, doi:10.1002/2016jg003455
- Hartl-Meier, C., C. Dittmar, C. Zang and A. Rothe 2014: Mountain forest growth response to climate change in the Northern Limestone Alps. – Trees **28** (3): 819-829, doi:10.1007/s00468-014-0994-1
- Heinrich, I., D. Balanzategui, O. Bens, G. Blasch, T. Blume, F. Bottcher, E. Borg, B. Brademann, A. Brauer, C. Conrad, E. Dietze, N. Drager, P. Fiener, H.H. Gerke, A. Guntner, I. Heine, G. Helle, M. Herbrich, K. Harfenmeister, K.U. Heussner, C. Hohmann, S. Itzerott, G. Jurasinski, K. Kaiser, C. Kappler, F. Koebsch, S. Liebner, G. Lischeid, B. Merz, K.D. Missling, M. Morgner, S. Pinkerneil, B. Plessen, T. Raab, T. Ruhtz, T. Sachs, M. Sommer, D. Spengler, V. Stender, P. Stuve and F. Wilken 2018: Interdisciplinary Geo-ecological Research across Time Scales in the Northeast German Lowland Observatory (TERENO-NE). – Vadose Zone Journal **17** (1), doi:10.2136/vzj2018.06.0116
- Hentschel, R., R. Hommel, W. Poschenrieder, R. Grote, J. Holst, C. Biernath, A. Gessler and E. Priesack 2016: Stomatal conductance and intrinsic water use efficiency in the drought year 2003: a case study of European beech. – Trees-Structure and Function **30** (1): 153-174, doi:10.1007/s00468-015-1284-2
- Herrmann, V., S.M. McMahon, M. Detto, J.A. Lutz, S.J. Davies, C.H. Chang-Yang and K.J. Anderson-Teixeira 2016: Tree Circumference Dynamics in Four Forests Characterized Using Automated Dendrometer Bands. – Plos One **11** (12): e0169020, doi:10.1371/journal.pone.0169020
- Hinckley, T.M., P.M. Dougherty, J.P. Lassoie, J.E. Roberts and R.O. Teskey 1979: A severe drought: Impact on tree growth, phenology, net photosynthetic rate and water relations. – American Midland Naturalist **102** (2), 307-316

- Ionita, M., L.M. Tallaksen, D.G. Kingston, J.H. Stagge, G. Laaha, H.A. Van Lanen, P. Scholz, S.M. Chelcea and K. Haslinger 2017: The European 2015 drought from a climatological perspective. – *Hydrology and Earth System Sciences* **21** (3): 1397-1419, doi:10.5194/hess-21-1397-2017
- Jolly, W.M., M. Dobbertin, N.E. Zimmermann and M. Reichstein 2005: Divergent vegetation growth responses to the 2003 heat wave in the Swiss Alps. – *Geophysical Research Letters* **32** (18): 1-4, doi:10.1029/2005GL023252
- Jucker, T., C. Grossiord, D. Bonal, O. Bouriaud, A. Gessler and D.A. Coomes 2017: Detecting the fingerprint of drought across Europe's forests: do carbon isotope ratios and stem growth rates tell similar stories? – *Forest Ecosystems* **4** (24): 1-11, doi:10.1186/s40663-017-0111-1
- Körner, C. 2012: Alpine treelines: functional ecology of the global high elevation tree limits. – Basel
- Latte, N., J. Perin, V. Kint, F. Lebourgeois and H. Claessens 2016: Major Changes in Growth Rate and Growth Variability of Beech (*Fagus sylvatica* L.) Related to Soil Alteration and Climate Change in Belgium. – *Forests* **7** (8): 1-15, doi:10.3390/f7080174
- MeteoSwiss 2015a: Klimabulletin Frühling 2015. – Zürich
- MeteoSwiss 2015b: Klimabulletin Sommer 2015. – Zürich
- MeteoSwiss 2016: Der Hitzesommer 2015 in der Schweiz. – Zürich
- MeteoSwiss 2018: Klimabulletin Sommer 2018. – Zürich
- Mullerova, J., V. Pejcha, J. Altman, T. Plener, P. Dorner and J. Dolezal 2016: Detecting Coppice Legacies from Tree Growth. – *Plos One* **11** (1): 1-14, doi:10.1371/journal.pone.0147205
- Muthers, S., G. Laschewski and A. Matzarakis 2017: The summers 2003 and 2015 in south-west Germany: Heat waves and heat-related mortality in the context of climate change. – *Atmosphere* **8** (11): 1-13, doi:10.3390/atmos8110224
- Nussbaumer, A., P. Waldner, S. Etzold, A. Gessler, S. Benham, I.M. Thomsen, B.B. Jorgensen, V. Timmermann, A. Verstraeten, G. Sioen, P. Rautio, L. Ukonmaanaho, M. Skudnik, V. Apuhtin, S. Braun and A. Wauer 2016: Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern Europe. – *Forest Ecology and Management* **363**: 237-251, doi:10.1016/j.foreco.2015.12.033
- Ogle, K., J.J. Barber, G.A. Barron-Gafford, L.P. Bentley, J.M. Young, T.E. Huxman, M.E. Loik and D.T. Tissue 2015: Quantifying ecological memory in plant and ecosystem processes. – *Ecology Letters* **18** (3): 221-235, doi:10.1111/ele.12399
- Pannatier, E.G., M. Dobbertin, A. Heim, M. Schmitt, A. Thimonier, P. Waldner and B. Frey 2012: Response of carbon fluxes to the 2003 heat wave and drought in three mature forests in Switzerland. – *Biogeochemistry* **107** (1-3): 295-317, doi:10.1007/s10533-010-9554-y
- Pretzsch, H., G. Schütze and P. Biber 2018: Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. – *Forest Ecosystems* **5** (20): 1-19, doi:10.1186/s40663-018-0139-x
- R Core Team 2016: R: a language and environment for statistical computing. – Wien
- Scharnweber, T., M. Manthey, C. Criegee, A. Bauwe, C. Schroder and M. Wilmking 2011: Drought matters – Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. – *Forest Ecology and Management* **262** (6): 947-961, doi:10.1016/j.foreco.2011.05.026
- Scherrer, S.C., E.M. Fischer, R. Posselt, M.A. Liniger, M. Croci-Maspoli and R. Knutti 2016: Emerging trends in heavy precipitation and hot temperature extremes in Switzerland. – *Journal of Geophysical Research-Atmospheres* **121** (6): 2626-2637, doi:10.1002/2015jd024634
- Shao, J., X. Zhou, Y. Luo, B. Li, M. Aurela, D. Billesbach, P.D. Blanken, R. Bracho, J. Chen, M. Fischer, Y. Fu, L. Gu, S. Han, Y. He, T. Kolb, Y. Li, Z. Nagy, S. Niu, W.C. Oechel, K. Pinter, P. Shi, A. Suyker, M. Torn, A. Varlagin, H. Wang, J. Yan, G. Yu and J. Zhang 2016: Direct and indirect effects of climatic variations on the interannual variability in net ecosystem exchange across terrestrial ecosystems. – *Tellus Series B – Chemical and Physical Meteorology* **68**: 1-16, doi:10.3402/tellusb.v68.30575
- Sterck, F. and F. Schieving 2011: Modelling functional trait acclimation for trees of different height in a forest light gradient: emergent patterns driven by carbon gain maximization. – *Tree Physiol* **31** (9): 1024-1037, doi:10.1093/treephys/tpr065
- Thomas, C.K., B.E. Law, J. Irvine, J.G. Martin, J.C. Pettijohn and K.J. Davis 2009: Seasonal hydrology explains interannual and seasonal variation in carbon and water exchange in a semiarid mature ponderosa pine forest in central Oregon. – *Journal of Geophysical Research-Biogeosciences* **114**: 1-22, doi:10.1029/2009jg001010
- van der Maaten-Theunissen, M., H. Bummerstede, J. Iwanowski, T. Scharnweber, M. Wilmking and E. van der Maaten 2016: Drought sensitivity of beech on a shallow chalk soil in northeastern Germany – a comparative study. – *Forest Ecosystems* **3** (24): 1-10, doi:10.1186/s40663-016-0083-6
- Vanoni, M., H. Bugmann, M. Notzli and C. Bigler 2016: Quantifying the effects of drought on abrupt growth decreases of major tree species in Switzerland. – *Ecology and Evolution* **6** (11): 3555-3570, doi:10.1002/ece3.2146
- Weemstra, M., B. Eilmann, U.G. Sass-Klaassen and F.J. Sterck 2013: Summer droughts limit tree growth across 10 temperate species on a productive forest site. – *Forest Ecology and Management* **306**: 142-149, doi:10.1016/j.foreco.2013.06.007

How did Swiss forest trees respond to the hot summer 2015?

- Wolf, S., T.F. Keenan, J.B. Fisher, D.D. Baldocchi, A.R. Desai, A.D. Richardson, R.L. Scott, B.E. Law, M.E. Litvak, N.A. Brunsell, W. Peters and I.T. van der Laan-Luijkx 2016: Warm spring reduced carbon cycle impact of the 2012 US summer drought. – Proceedings of the National Academy of Science of the United States of America **113** (21): 5880-5885, doi:10.1073/pnas.1519620113
- Zielis, S., S. Etzold, R. Zweifel, W. Eugster, M. Haeni and N. Buchmann 2014: NEP of a Swiss subalpine forest is significantly driven not only by current but also by previous year's weather. – Biogeosciences **11**: 1627-1635, doi:10.5194/bg-11-1627-2014
- Zweifel, R., W. Eugster, S. Etzold, M. Dobbertin, N. Buchmann and R. Häsler (2010): Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps. – New Phytologist **187**: 819-830, doi:10.1111/j.1469-8137.2010.03301.x
- Zweifel, R., M. Haeni, N. Buchmann and W. Eugster (2016): Are trees able to grow in periods of stem shrinkage? – New Phytologist **211**: 839-849, doi:10.1111/nph.13995
- Zweifel, R. and F. Sterck (2018): A conceptual tree model explaining legacy effects on stem growth. – Frontiers in Plant Sciences **1** (9): 1-9, doi:10.3389/ffgc.2018.00009