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Contrasting responses of forest growth and carbon sequestration to heat and drought in the Alps

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Contrasting responses of forest growth and carbon sequestration to heat and drought in the Alps

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Consolata Siniscalco¹, Umberto Morra di Cella⁴ and Marta Galvagno^{4,*} ¹ University of Torino, Department of Life Sciences and Systems Biology, Torino, Italy² Max Planck Institute for Biogeochemistry, Jena, Germany³ European Commission, Joint Research Center, Ispra, Italy⁴ Environmental Protection Agency of Aosta Valley, Climate Change Unit, ARPA VdA, Aosta, Italy⁵ Università Degli Studi di Milano, Department of Agricultural and Environmental Sciences, Milano, Italy

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E-mail: m.galvagno@arpa.vda.it**Keywords:** climate extremes, eddy covariance, mountain forests, european larch, tree growth, carbon cycleSupplementary material for this article is available [online](#)**Abstract**

Climate change is expected to increase both the frequency and the intensity of climate extremes, consequently increasing the risk of forest role transition from carbon sequestration to carbon emission. These changes are occurring more rapidly in the Alps, with important consequences for tree species adapted to strong climate seasonality and short growing season. In this study, we aimed at investigating the responses of a high-altitude *Larix decidua* Mill. forest to heat and drought, by coupling ecosystem- and tree-level measurements. From 2012 to 2018, ecosystem carbon and water fluxes (i.e. gross primary production, net ecosystem exchange, and evapotranspiration) were measured by means of the eddy covariance technique, together with the monitoring of canopy development (i.e. larch phenology and normalized difference vegetation index). From 2015 to 2017 we carried out additional observations at the tree level, including stem growth and its duration, direct phenological observations, sap flow, and tree water deficit. Results showed that the warm spells in 2015 and 2017 caused an advance of the phenological development and, thus, of the seasonal trajectories of many processes, at both tree and ecosystem level. However, we did not observe any significant quantitative changes regarding ecosystem gas exchanges during extreme years. In contrast, in 2017 we found a reduction of 17% in larch stem growth and a contraction of 45% of the stem growth period. The growing season in 2017 was indeed characterized by different drought events and by the highest water deficit during the study years. Due to its multi-level approach, our study provided evidence of the independence between C-source (i.e. photosynthesis) and C-sink (i.e. tree stem growth) processes in a subalpine larch forest.

1. Introduction

Projections of future climate change indicate that extreme events will be more frequent and intense with every additional increment of global warming (Seneviratne *et al* 2021). This trend was already observed in Europe, with unusually hot periods in summer and severe drought events (Schär *et al* 2004, Ciais *et al* 2005, Cremonese *et al* 2017, Chiogna *et al* 2018, Peters *et al* 2020, Stephan *et al* 2021). Climate

extremes have the potential to alter ecosystem processes significantly (Jentsch *et al* 2011), with major effects on carbon cycling and long-term continental carbon balance (Ciais *et al* 2005, Reichstein *et al* 2013, Baldocchi *et al* 2018, Von Buttlar *et al* 2018, Sippel *et al* 2018a). Nevertheless, due to the plethora of responses exhibited by each ecosystem process towards different types of extremes, there is still a lack of knowledge about the impacts of heatwaves and droughts on carbon sequestration and thus on

climate change mitigation potential of different terrestrial ecosystems.

It has been estimated that since 1750, forests sequestered from the atmosphere about half of the carbon emissions (Ciais *et al* 2005). Despite their fundamental role in carbon sequestration, the future of forests under climate change remains highly uncertain (Anderegg *et al* 2015). Forests, and especially montane forests, were considered resilient ecosystems for a long time, due to their long-term adaptation to extreme climatic conditions, and high genetic and structural diversity (e.g. Butler *et al* 1994, Masek 2001). By contrast, more recent studies highlighted forest vulnerability to increasing climate variability, which may strongly affect forest ecosystem processes and dynamics (e.g. Ciais *et al* 2005, Bréda *et al* 2006, Allen *et al* 2010, Choat *et al* 2012, Piayda *et al* 2014), potentially leading to forest role transition from carbon sequestration to carbon emission at local and regional scale (Ciais *et al* 2005, Kurz *et al* 2008, Gatti *et al* 2021).

Most of the recent interannual variability of carbon fluxes in forests is dominated by climate extremes, especially drought events (Reichstein *et al* 2013, Wei *et al* 2014, Zscheischler *et al* 2014). Moreover, the occurrence of compound extremes, referred to as simultaneous, concurrent, or coincident extremes, has important consequences on ecosystem processes (De Boeck *et al* 2016).

In particular, forest responses during drought events are mediated by complex mechanisms and trade-offs between carbon gain and water loss. These mechanisms act at tree-level and are mainly driven by a continuum of stomatal responses from drought avoidance (i.e. 'isohydric' species minimize transpiration and maintain a relatively constant leaf water potential) to drought tolerance (i.e. 'aniso-hydric' species maintain their transpiration rate and allow leaf water potential to decline) (e.g. Zweifel *et al* 2009, Aubin *et al* 2016, Martínez-Vilalta and Garcia-Forner 2017). Stomatal regulation affects not only water loss but also carbon assimilation through photosynthesis, which represents the carbon source (C-source) for a plant and determines gross primary production (GPP). According to the hypothesis of a C-source limitation, GPP limits plant growth. However, recent studies highlighted that plant growth may be limited by other factors than carbon assimilation, such as environmental or plant internal controls, which have the potential to alter plant growth (C-sink) processes (e.g. tissue expansion and meristematic activity, autotrophic respiration and root exudation) (Fatichi *et al* 2014, 2019, Hartmann *et al* 2020, Eckes-Shephard *et al* 2021).

Furthermore, forest exposure to climate change and its consequences on ecosystem structure and function differ across Europe, according to bioclimatic zones (Lindner *et al* 2010). Alpine ecosystems have been shown to be more sensitive to climate

change. In fact, in recent decades, the average temperatures in the Alps increased more rapidly than the global trend (Gobiet *et al* 2014, Obojes *et al* 2018, Abram *et al* 2019). The consequences of climate change will be especially critical in dry inner alpine regions of central Europe, eventually leading to changes in tree species composition and treeline expansion (Körner 2012, Greenwood and Jump 2014, Obojes *et al* 2018, Thom and Seidl 2021).

European larch (*Larix decidua* Mill.) is one of the most important and valuable tree species in the Alps, and it is naturally most abundant above 1500 m asl up to the tree line. The deciduous behaviour of European larch, the only deciduous conifer in Europe, has been interpreted as an adaptation to cold alpine climates since the absence of leaves during winter reduces desiccation damage on foliage (da Ronch *et al* 2016). In particular, European larch shows high transpiration rates, which are maintained during short drought events, due to its aniso-hydric strategy, especially at the higher altitudes (Anfodillo *et al* 1998, Badalotti *et al* 2000, Wieser 2012, Leo *et al* 2014, Obojes *et al* 2018). Differently from isohydric conifer species, such as *Picea abies*, *Pinus sylvestris*, and *Abies alba*, which suffer more but recover quicker under short drought events, aniso-hydric species, such as *L. decidua*, may suffer more during long-lasting drought events due to the impairment of tree water status (Bréda *et al* 2006, McDowell *et al* 2008, Hartmann 2011).

Although many studies exist on different larch species' responses to environmental fluctuations (e.g. Dulamsuren *et al* 2010, Zhang *et al* 2016, Danek *et al* 2018, Vitasse *et al* 2019), to our knowledge, no field-based studies on European larch forests coupling direct measurements of tree physiology and ecosystem processes have been published yet. In this study, we used a multi-level approach by coupling a variety of measurements at the scale of individual trees (i.e. tree ring widths, sap flow, phenology) and of the whole ecosystem (i.e. CO₂ and water fluxes, NDVI), to monitor various aspects of the forest functioning and growth. Our main aim was to describe the tree-level responses to heat and drought occurring with different timing and magnitude, and to investigate the relations among tree and ecosystem responses.

In this study, we aimed at answering the following questions: (a) How do European larch forests cope with climate extremes at high elevation? (b) Are the larch responses in line with the responses at the ecosystem level? (c) What is the relation between C-source (i.e. photosynthesis) and C-sink (i.e. tree growth) processes, during climate extremes?

2. Materials and methods

2.1. Study site

The study was carried out in a mountain forest located in the western Italian Alps, at an elevation of

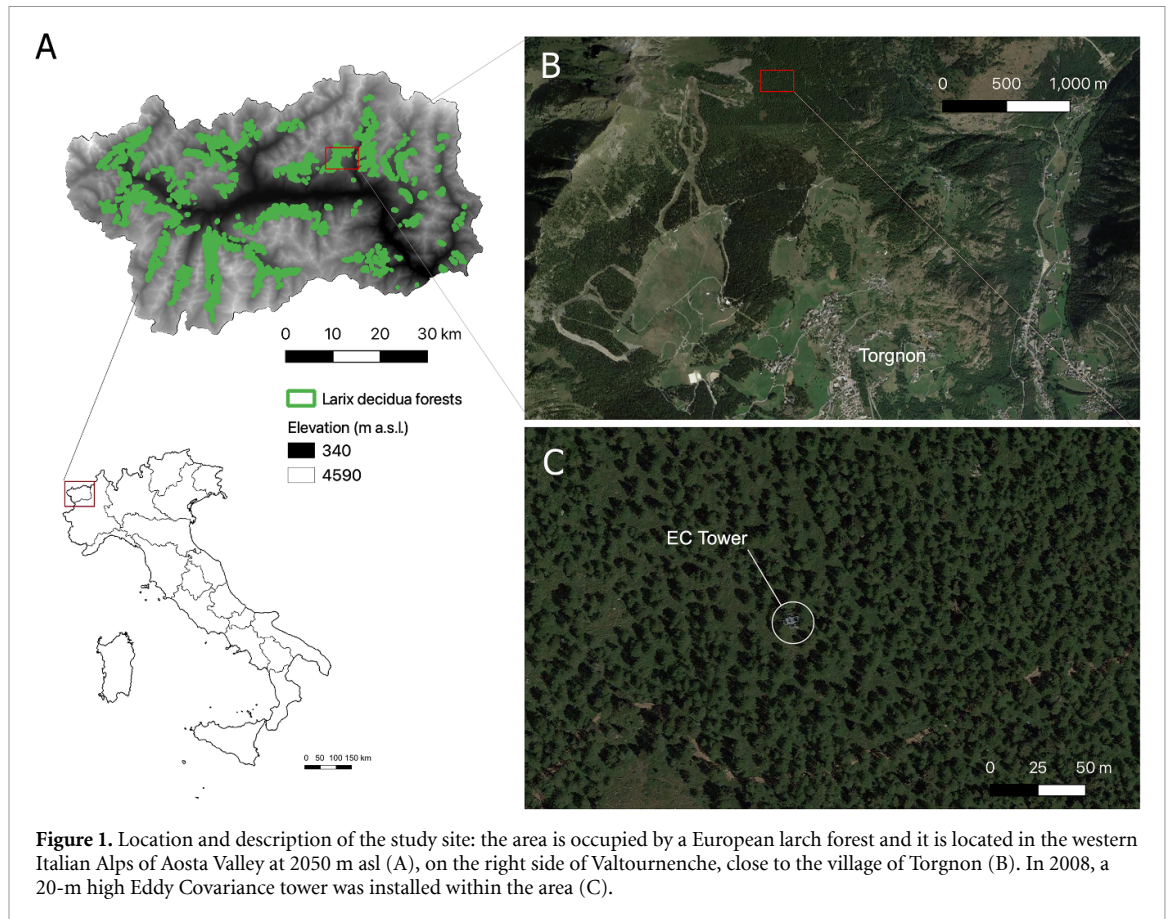


Figure 1. Location and description of the study site: the area is occupied by a European larch forest and it is located in the western Italian Alps of Aosta Valley at 2050 m asl (A), on the right side of Valtournenche, close to the village of Torgnon (B). In 2008, a 20-m high Eddy Covariance tower was installed within the area (C).

2050 m asl (IT-TrE, $45^{\circ} 49'23.38''\text{N}$, $7^{\circ} 33'39.04''\text{E}$, figure 1). The forest has an open canopy structure and the tree stratum is dominated (92% of relative abundance as percent cover) by European larch (*Larix decidua* Mill.) with sporadic (8%) Norway spruce (*Picea abies* (L.) H.Karst) individuals. Larch trees have mean height of 11.7 ± 4 m, mean age of 155 years, and maximum LAI around $3.5 \text{ m}^2 \text{ m}^{-2}$. Larch trees have no needles during dormancy, from early November to April/May. The understory is mainly composed by shrub species (*Juniperus communis* Willd., *Rhododendron ferrugineum* L., *Vaccinium myrtillus* L., *V. vitis-idaea* L. and *V. uliginosum* L.) and some herbaceous species such as *Arnica montana* L., *Pulsatilla alpina* (L.) Delarbre, *Trifolium alpinum* L. and *Festuca varia* Haenke. Regarding climate, the site is characterized by cold winters (mean air temperature around -2°C) and mild summers (mean air temperature around 12°C), and annual precipitation of about 880 mm.

2.2. Biometeorological measurements

Air temperature and relative humidity were measured with a HMP45 sensor (Vaisala Inc. Helsinki, Finland) installed 20 m above the tree canopy. Net radiation was measured with a CNR4 (Kipp and Zonen, Delft the Netherlands) net radiometer and precipitation was assessed with OTT Pluvio2 rain

gauge (OTT HydroMet GmbH Kempten, Germany). All the biometeorological variables were measured at 30-min intervals and raw data were used to calculate daily and monthly averages and standard deviations. Finally, long-term mean air temperature and cumulative precipitation values were computed on the basis of data collected from 1950 to 2018 at a nearby meteorological station ($45^{\circ} 52'31''\text{N}$, $7^{\circ} 35'19''\text{E}$, Cignana, Meteorological Service of Aosta Valley) located at the same altitude of the study site. The occurrence of climatic anomalies was investigated through the calculation of two indices: vapor pressure deficit and water deficit (Gao *et al* 2018, 2020).

2.3. Canopy development

Seasonal canopy development was tracked with the integration of proximal sensing data and field observations. Proximal sensing data were measured with SKR1800 sensors (Skye Instruments) collecting spectral signatures of the canopy: red (central wavelength: 640 nm, bandwidth: 50 nm) and near-infrared (central wavelength: 860 nm, bandwidth: 40 nm) bands. Spectral data were used to compute the Normalized Difference Vegetation Index (NDVI), a commonly used vegetation index related to canopy structure and phenology. Finally, direct observations of larch needle phenology have been performed at the study site since 2010 on three plots with ten individuals each, located

inside the eddy covariance footprint. One of the three plots is located inside the NDVI field of view. The protocol used for these observations was described in (Migliavacca *et al* 2008), which provides information on budburst (SP2), full needle formation (SP5) and beginning of needle senescence (AP1).

2.4. Tree level observations: stem growth, sap flow and tree water deficit

Sap flow was measured at four individual larches, located at a minimum reciprocal distance of 10 m, with thermal dissipation probes (Granier 1985), model SFS2 (UP GmbH, Germany), from 2015 to 2017. The probes had a length of 33 mm and were installed at breast height (1.3 m from the soil), inserted radially for 25 mm into the trunk. On each tree, two pairs of thermocouples were installed and connected to a data logger for data recording at 10-min intervals. The sap flux density, (F_d , $\text{g m}^{-2} \text{s}^{-1}$), was calculated following the equation derived by Granier (1985, 1987), as the temperature difference between the two probes (ΔT) relative to the maximum temperature difference, ΔT_{max} , which occurs when the sap flow is null. The ΔT_{max} value was calculated using the 'TRACC' algorithm proposed by Ward *et al* (2017), with a vapor pressure deficit threshold of 4.5 hPa. To calculate the sap flux density, we used the equation below (equation (1)), where K is the ratio between ($\Delta T_{\text{max}} - \Delta T$) and ΔT . Moreover, ΔT value in equation (1) was corrected according to Clearwater *et al* (1999), in order to account for the probe portion located in the heartwood, which, contrary to the sapwood, is not active in the water transport.

$$F_d = 119 \times K^{1.231} \quad [\text{g m}^{-2} \text{s}^{-1}]. \quad (1)$$

Retrospective analysis of aboveground carbon sink was carried out by measuring annual tree ring series from a sample of trees at the site of study. The evaluation of the tree ring widths was carried out in summer 2020 in 15 plots randomly located across the study site and falling in the eddy covariance flux footprint. Fifty trees within a 1-ha area were randomly chosen among all stem diameter classes and cored with an increment borer. Two cores were extracted for each tree at breast height, and tree height and stem diameter at breast height were also measured. Tree cores were prepared according to standard dendrochronological techniques and scanned. Tree ring widths were measured, cross-dated, and averaged for each tree using Cybis CooRecorder 7.1 (Cybis Elektronik & Data AB, Sweden). Ring widths series were converted to inside-bark stem diameter series using measured diameters. Diameter series were then converted to aboveground biomass series by applying allometric equations based on tree height and diameter (Tabacchi *et al* 2011), and then to tree-level carbon increments by applying a carbon density coefficient of 0.47 g g^{-1} . Finally, we calculated the mean

series intercorrelation (0.56) and the expressed population signal (EPS = 0.93), based on Cook and Pederson (2011) and Buras (2017), which reflect that the sampled chronology well represents a theoretically infinite population.

2.5. Ecosystem gas exchanges

Measurements of H_2O and CO_2 fluxes were carried out since 2012 by means of the eddy covariance technique to quantify ecosystem evapotranspiration (ET), net ecosystem exchange (NEE), and the derived gross primary production (GPP) (Baldocchi 2003). The instrumental setup consists of an eddy covariance system installed at 20 m above the tree canopy. The system includes a three-dimensional sonic anemometer (CSAT3, Campbell Sci.) for the measurements of wind speed in the three components (u , v , w) and the sonic temperature, and a LI-7500 open-path infrared gas analyser (LI-COR, Inc.) for the measurements of CO_2 and H_2O densities (mmol m^{-3}). Half-hourly eddy fluxes were calculated from raw data recorded at 10 Hz frequency, following the standard procedures (Aubinet 2012) implemented in the EddyPro software (LI-COR, Inc.). Gap-filling method to obtain the daily and longer time-scale sums of H_2O and CO_2 exchanges, and the partitioning of measured NEE in its component fluxes (i.e. GPP and Ecosystem Respiration), were performed by the implementation of the methods described in Reichstein *et al* (2005) using the 'REddyProc' R package (Wutzler *et al* 2018). For convention, negative values of NEE indicate net CO_2 uptake and positive values net CO_2 emissions. In the following section, the term NEP (Net Ecosystem Production) will be used, which equals NEE but it is opposite in sign.

2.6. Data analysis

All the analyses were carried out on a subset of data falling into the larch growing season (i.e. April–October), which was defined on the basis of the phenological observations carried out from 2012 to 2018. The beginning and the end of the growing season were respectively set at the DOY (Day of the Year) of the earliest budburst and the latest onset of needle senescence, as observed in the field, in order to avoid the exclusion of any seasonal trajectory segments. Biometeorological data, as well as tree-level measurements, ecosystem phenological indices and gas exchange data were analysed to calculate daily mean (air temperature, vapour pressure deficit, sap flow, tree water deficit) or daily cumulative values (precipitation, water deficit, tree stem growth, GPP, NEP and ET) for all the study years. Daily mean or cumulative values of all the different variables were then averaged or summed in order to calculate the daily mean or cumulative values of each variable during the growing season (April–October). Although the study had been carried out from 2012 to 2018, tree-level measurements were performed only during 2015, 2016, and

2017, and thus, the analyses mainly focused on the differences among these three years.

Seasonal trajectories of gas exchange data were analysed using the 'phenopix' R package (Filippa *et al* 2016) by fitting the data with a double logistic function, following the formula proposed by Gu *et al* (2003). The fitting equations and their parameters were used to extract the 'Maxline', defined as the horizontal line corresponding to the maximum of the curve (i.e. seasonal peak) (Gu *et al* 2009). The differences among years were tested for significance using generalized linear models (GLMs) followed by Tukey's HSD post hoc test for multiple comparisons, with single-step method to calculate adjusted *p*-values (95% CI). Correlation between variables was tested through the Winsorized correlation test (Mair and Wilcox 2019).

Finally, the anomalies of vapor pressure deficit, water deficit, GPP and tree growth were calculated for each study year by comparing the daily mean value of each growing season with the daily mean value of all the study years (2012–2018).

Statistical analysis and figure creation were performed using R 4.1.1 (R Core Team 2021).

3. Results

3.1. Biometeorological factors

Long-term data (1950–2018) of daily mean air temperature and cumulative precipitation, which were calculated from April to October (i.e. growing season), showed a general trend of increasing air temperature, with 2015, 2017 and 2018 being the only years with daily mean air temperature higher than 10.0 °C since 1950 (figure 2(A)). Except for 2012, the years of the study (i.e. 2012–2018) grouped and stood out mainly due to their higher daily mean air temperature (9.8 ± 1.0 °C) compared to previous years (7.0 ± 1.6 °C). Regarding precipitation, data were more variable, and we did not observe a trend over time. Nevertheless, 2017 was the sixth driest year from 1950 and the driest among the study years (figure 2(A)).

The biometeorological data collected at the study site allowed us to analyse more deeply the climatic fluctuations of the investigated years and to quantitatively describe the anomalies through the calculation of the vapor pressure (VPD) and water (WD) deficit indices (figures 2(B) and (C)). VPD showed the highest daily mean value in 2017 (4.9 hPa), followed by 2018 (4.1 hPa) and 2015 (4.0 hPa). Regarding water deficit, 2017 was the only year showing negative values of PRC-ET, with a reduction of 175% in WD values, compared to the 2012–2018 average. Moreover, 2017 was also the driest year in the study site, with 410.5 mm of cumulative precipitation. Finally, we tested the VPD and WD differences among years, and we observed that 2017 was significantly (95% CI) different from all the other years of the study, showing

the highest VPD and the lowest WD anomaly from 2012 to 2018.

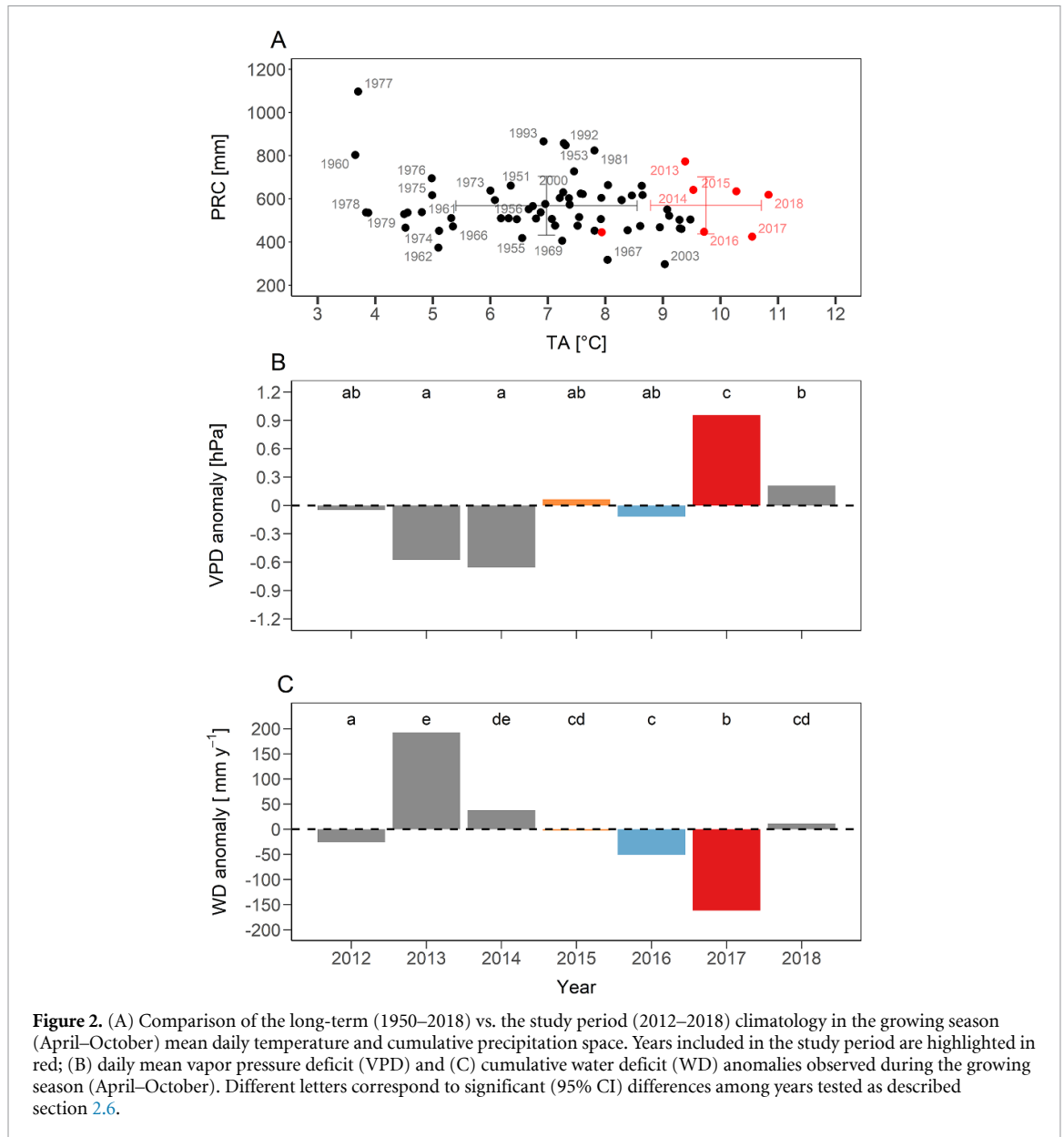
3.2. Tree-level responses: phenology, stem growth and tree water balance

The analyses of the phenological data allowed us to highlight an advance of all the three main monitored phenophases (i.e. (SP2) budburst, (SP5) full needle formation, and (AP1) onset of needle senescence) during 2015 and 2017, which were also characterized by an earlier snowmelt. During 2015 and 2017, the budburst occurred about one week earlier than 2016, and full needle formation was reached at DOY 185 and 176 in 2015 and 2017, respectively, whereas it occurred at DOY 192 in 2016. Similarly, needle senescence began almost two weeks earlier in 2015 and 2017 (table 1; figure 3). The phenological advance that occurred in 2015 and 2017 was also confirmed by comparing the mean date of phenophase occurrence calculated for all the study years (i.e. 2012–2018) (data not shown).

We then used the phenophase dates to calculate the daily mean VPD and cumulative WD during three phenological intervals: (1) from snowmelt to SP2 (i.e. from snowmelt to budburst), (2) from SP2 to SP5 (i.e. needle elongation), and (3) from SP5 to AP1 (i.e. full needle formation until the onset of senescence). The analyses highlighted a significantly higher VPD daily mean value (5.9 ± 3.1 hPa) during needle elongation in 2017 compared to 2015 (4.3 ± 2.2 hPa) ($df = 132$; p -value < 0.05) and 2016 (3.9 ± 2.5 hPa) ($df = 132$; p -value < 0.01). Moreover, 2015 showed the highest mean VPD value before budburst (3.8 ± 3.1 hPa), but the difference with the other years was not significant (figure 3(A)). These findings were consistent with the differences relative to the daily mean air temperature, that between snow melt and budburst was significantly higher in 2015 (7.0 ± 3.6 °C), compared to 2016 (3.7 ± 2.1 °C) and 2017 (1.7 ± 3.7 °C) ($df = 132$; p -value < 0.01). Differently, during needle elongation (i.e. from SP2 to SP5) 2017 showed the highest daily mean air temperature (11.9 ± 3.8 °C), followed by 2015 (9.8 ± 9.8 °C) and 2016 (9.6 ± 9.5 °C) ($df = 132$; p -value < 0.05). Although we did not find any significant difference, we observed that 2017 showed the highest water deficit from budburst to full needle senescence and that the cumulative daily WD average remained negative also during the following phenological interval (figure 3(B)).

The temporal shift observed for the phenophases was even more remarkable when considering tree growth (i.e. stem radial increment) that started one month and three weeks earlier in 2015 and 2017 respectively, compared to 2016. Although the earlier onset, in 2017 the tree growth period lasted barely 54 days, which was 45% shorter compared to both 2015 and 2016 (table 1; figure 3(C)).

Although larch growth started earlier in both 2015 and 2017, the stem radial increment, as measured



by dendrometers, followed two different patterns (figure 4(A)). In 2015, we observed an exponential increase until the end of August (DOY 236), whereas in 2017 larch growth slowed down prior to halt in mid-August (DOY 223). These differences, that were found to be significant ($df = 364$; p -value < 0.01) among all the three years, led to a higher and a lower annual stem growth respectively in 2015 (0.55 mm) and 2017 (0.34 mm), compared to 2016 (0.43 mm) (figure 4(A)). Regarding sap flow, we observed that the seasonal trajectory started earlier in 2015 and 2017. The daily mean value during the growing season was higher in 2015 (0.26 g s^{-1}), followed by 2017 (0.22 g s^{-1}) and 2016 (0.18 g s^{-1}) (figure 4(B)).

Finally, we found evidence of water stress in 2017, during which trees showed a significantly lower value of daily mean TWD (-0.18 mm d^{-1}) compared to 2015 and 2016 (-0.03 mm d^{-1}) ($df = 625$;

p -value < 0.001). Moreover, 2017 showed also the lowest daily minimum TWD (-0.48 mm d^{-1}) compared to 2015 and 2016 whose minimum value was around -0.14 mm d^{-1} (figure 4(C)).

3.3. Ecosystem-level responses: phenology and gas exchanges

Regarding canopy development, NDVI values (supplementary figure S1 available online at stacks.iop.org/ERL/17/045015/mmedia) confirmed an advance of the seasonal trajectories in 2015 and 2017, compared to 2016. Nevertheless, no significant differences were found among years. During the growing season, the mean daily NDVI was 0.53 ± 0.01 in both 2015 and 2017 and 0.51 ± 0.01 in 2016. The maximum daily NDVI values were 0.80 in 2015 and 2016 and 0.81 in 2017.

Table 1. DOY (Day Of the Year) of occurrence of (SM) snowmelt, (SP2) budburst, (SP5) full needle formation and (AP1) onset of needle senescence, and DOY of occurrence of (GRO_{beg}) tree growth beginning and (GRO_{end}) tree growth end, during 2015, 2016 and 2017 in a subalpine larch forest. Uncertainty is represented for each variable as the standard deviation of the day of occurrence among the sampled tree individuals.

Year	SM	SP2	SP5	AP1	GRO _{beg}	GRO _{end}
2015	116	138 ± 7.3	185 ± 3.4	276 ± 6.4	162 ± 2.1	262 ± 1.0
2016	124	144 ± 5.6	192 ± 3.0	288 ± 4.9	192 ± 0.6	290 ± 0.5
2017	105	136 ± 11.0	176 ± 4.6	276 ± 7.9	170 ± 3.0	224 ± 0.73

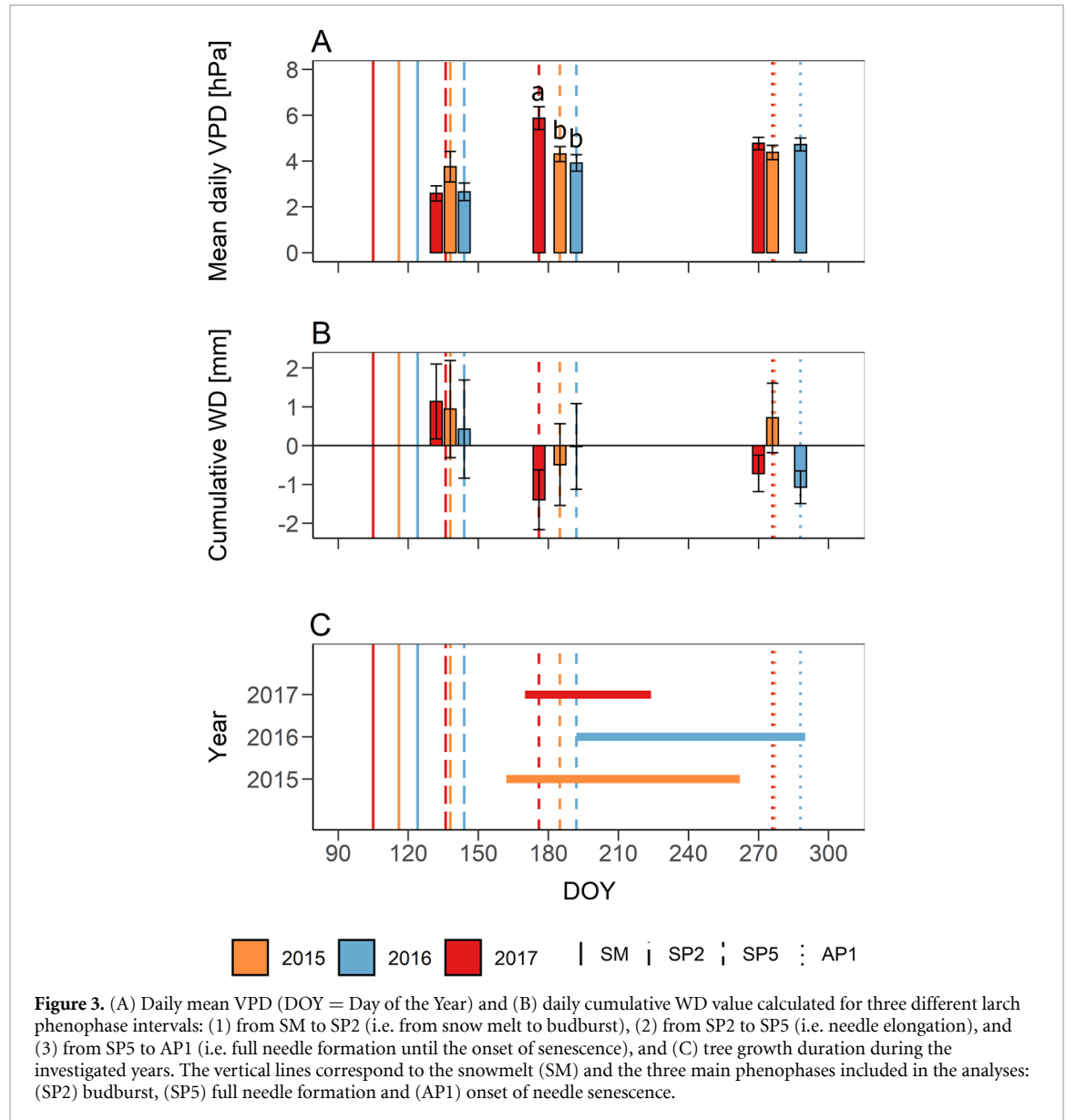


Figure 3. (A) Daily mean VPD (DOY = Day of the Year) and (B) daily cumulative WD value calculated for three different larch phenophase intervals: (1) from SM to SP2 (i.e. from snow melt to budburst), (2) from SP2 to SP5 (i.e. needle elongation), and (3) from SP5 to AP1 (i.e. full needle formation until the onset of senescence), and (C) tree growth duration during the investigated years. The vertical lines correspond to the snowmelt (SM) and the three main phenophases included in the analyses: (SP2) budburst, (SP5) full needle formation and (AP1) onset of needle senescence.

Focusing on gas ecosystem exchanges, we observed an advance of the GPP, NEP and ET seasonal trajectories (supplementary figure S2). Regarding the seasonal mean, 2016 showed the highest daily values of GPP (6.4 gC m^{-2}) and NEP (3.3 gC m^{-2}), followed by 2015 and 2017 (supplementary figure S2). The total amount of ET from April to October was 508.6, 437.1, and 476.6 mm in 2015, 2016, and 2017, respectively. The total amount of NEP and GPP showed the highest value in 2016, followed by 2015 and 2017 (see table 2 for more details).

To explore the link between C-source and C-sink processes, we investigated the relationship between the ecosystem GPP and the tree stem growth. We included in this analysis all the years for which GPP and tree growth data were available, from 2012 to 2018. Figure 5 shows the comparison between stem growth and GPP interannual variability. The results showed that tree stem increment was significantly lower in 2017, with a negative anomaly of 1 gC tree^{-1} (-17%) compared to the mean of the study years (5.8 gC tree^{-1}) (figure 5(A)). Conversely, we did not

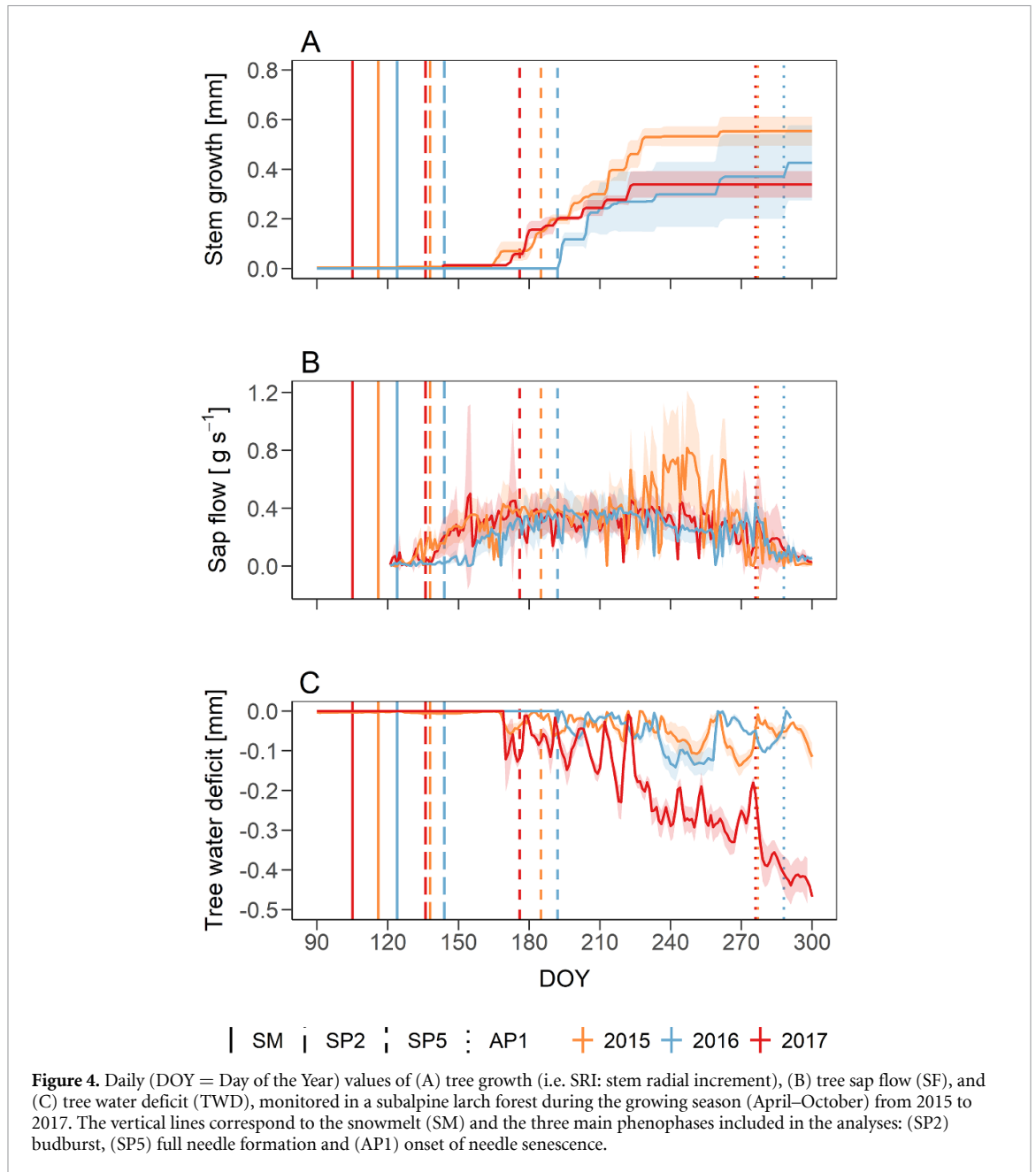


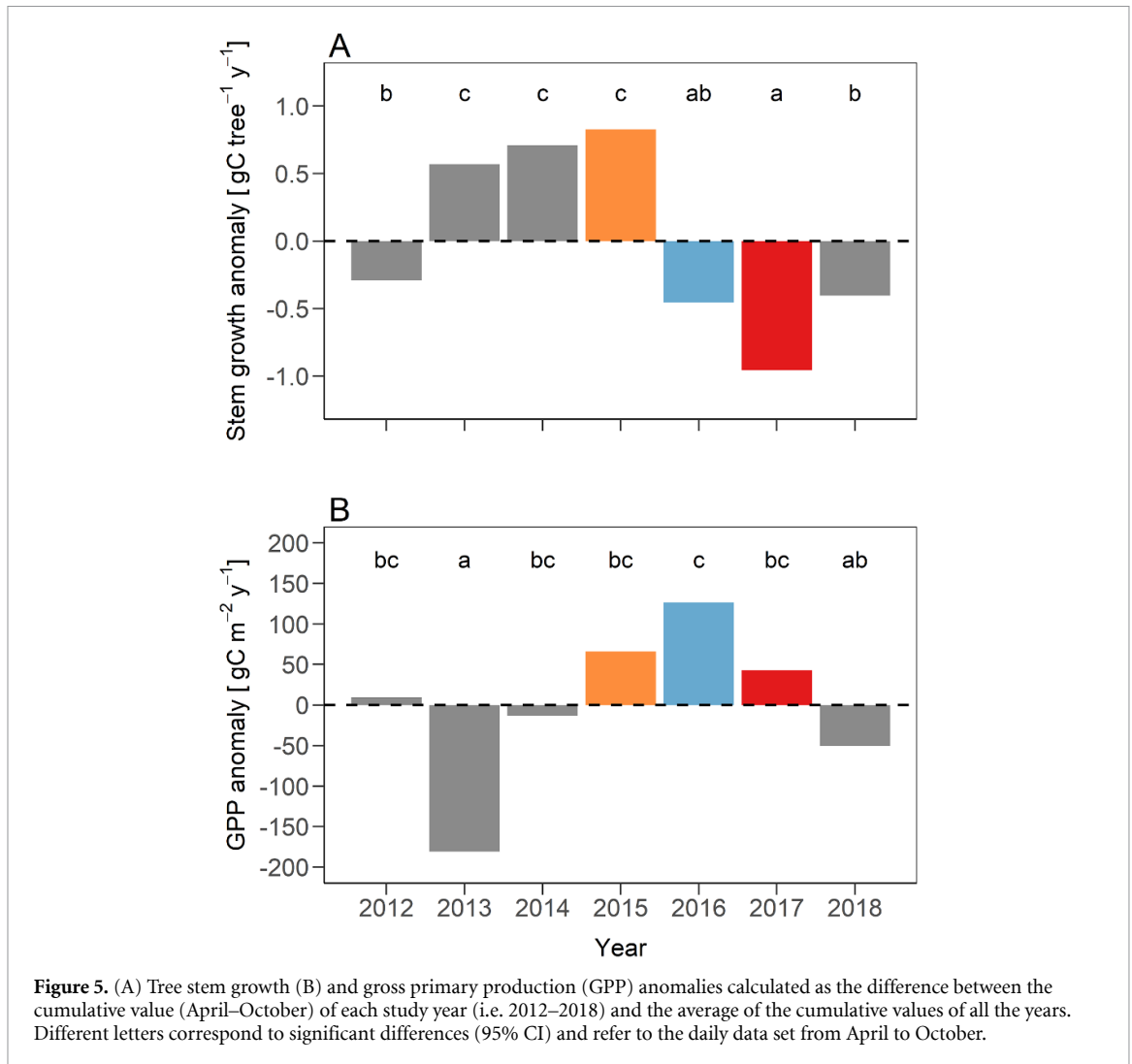
Figure 4. Daily (DOY = Day of the Year) values of (A) tree growth (i.e. SRI: stem radial increment), (B) tree sap flow (SF), and (C) tree water deficit (TWD), monitored in a subalpine larch forest during the growing season (April–October) from 2015 to 2017. The vertical lines correspond to the snowmelt (SM) and the three main phenophases included in the analyses: (SP2) budburst, (SP5) full needle formation and (AP1) onset of needle senescence.

Table 2. Daily mean values of ecosystem gas exchanges calculated by averaging daily cumulative GPP, NEP and ET data of the growing season (April–October), from 2015 to 2017 in a subalpine larch forest. Uncertainty is represented for each variable as the standard deviations among different gap-filling and partitioning methods available to compute fluxes (see section 2.5).

Year	GPP		NEP		ET	
	Daily mean	Sum	Daily mean	Sum	Daily mean	Sum
2015	6.1 ± 0.84	1278.5 ± 111.0	3.2 ± 0.65	694.9 ± 111.6	2.4 ± 0.07	508.6 ± 12.0
2016	6.4 ± 0.90	1338.7 ± 126	3.3 ± 0.67	708.9 ± 125.3	2.2 ± 0.08	437.1 ± 15.3
2017	6.0 ± 0.80	1255.1 ± 105	3.2 ± 0.63	678.3 ± 105.0	2.2 ± 0.06	476.6 ± 8.0

observe the same pattern for ecosystem GPP that in 2017 showed a positive anomaly and did not differ significantly from any other year, except for 2013 (figure 5(B)). Correlation test and regression models validated the absence of a significant relationship between GPP and stem growth (figure 6(C)). Similarly, NEP was not significantly correlated with stem

growth (figure 6(D)). Finally, GPP and stem growth showed a different correlation pattern with growing season length, since the former showed a positive significant correlation ($\rho_w = 0.79$; $H = 2.89$; p -value < 0.05) that instead was not observed for growth ($\rho_w = -0.42$; $H = -1.03$; p -value = 0.35) (figures 6(A) and (B)).



4. Discussion

Climate extreme events have the potential to alter forest ability to sequester CO₂ from the atmosphere and to store it as plant biomass. In this study we took advantage of naturally occurred warm and drought spells to analyse the multiple responses of a subalpine European larch forest to extreme events by coupling ecosystem- to tree-based observations in the field.

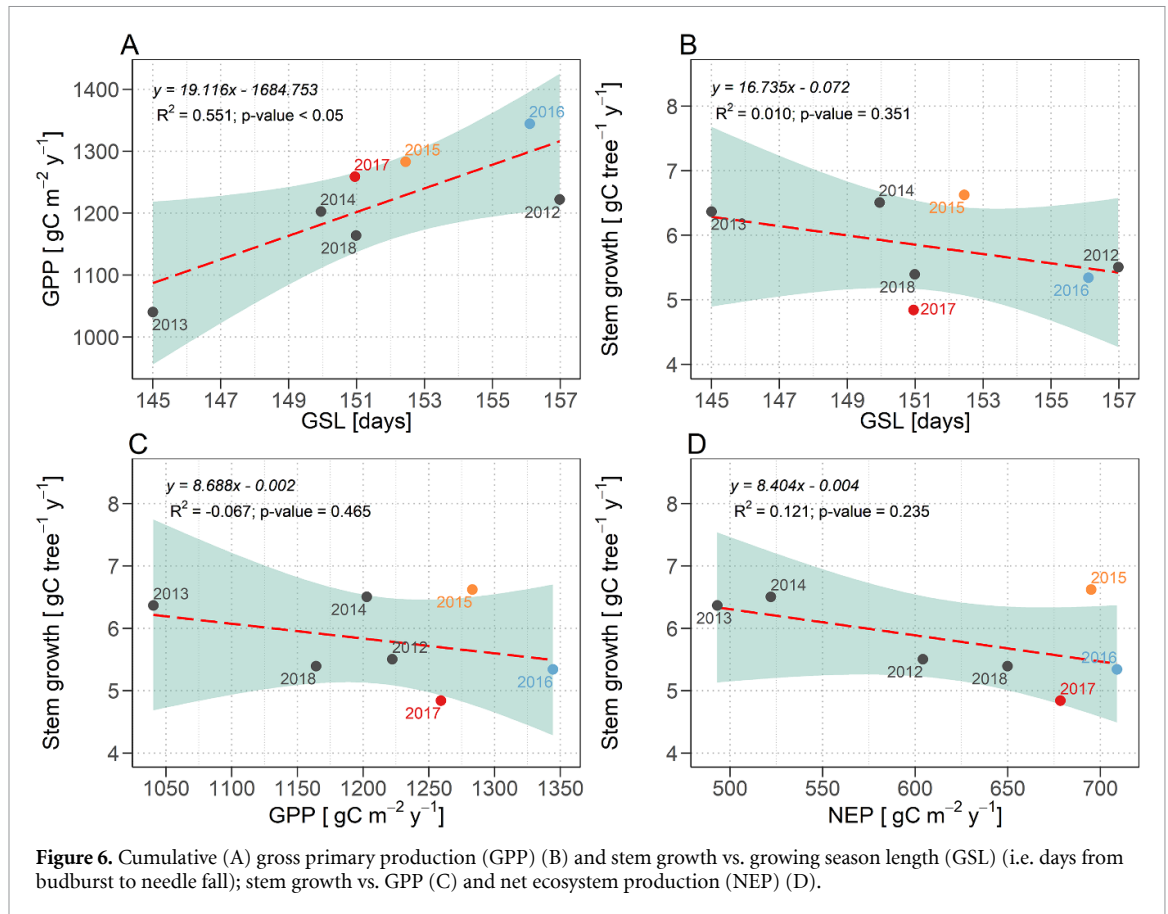
On one side, the higher temperatures observed during two of the study years (i.e. 2015 and 2017) mainly altered tree and ecosystem phenology, leading to a general advance of many investigated processes. On the other side, the drought event observed in 2017 did not lead to any significant consequences for the total amount of GPP and NEP, but had a significant impact on tree-level processes. Thanks to the multi-level approach applied in this study, we highlighted that C-source (i.e. carbon fixed through photosynthesis) and C-sink (i.e. carbon investment in plant growth) processes responded differently to climate extremes, since they are supposed to be differently driven by environmental factors (Fatichi *et al* 2014, 2019).

4.1. How do European larch forests cope with climate extremes at high elevation?

Our results showed that the heat and drought events occurred in 2015 and 2017 altered the timing of several forest processes with different impacts at the tree vs. ecosystem level.

In particular, we found an earlier onset of ecosystem fluxes and canopy development during the growing seasons of 2015 and 2017, likely due to the early spring high temperatures registered at the study site (Wolf *et al* 2016, Xie *et al* 2018, Xu *et al* 2020). It is well known that budburst and growth onset after winter dormancy in temperate and boreal trees are highly responsive to temperature (Migliavacca *et al* 2008, Hänninen and Tanino 2011). Similarly, warmer spring temperatures may alter temporal dynamics of wood formation resulting in an earlier onset of cambial activity and xylem cell differentiation (Oberhuber *et al* 2014).

However, the temporal shift observed in the seasonal trajectories did not cause a significant reduction neither in the rate or amount of ecosystem carbon sequestration, nor in the amount of (evapo)transpired water as also confirmed by tree



sap flow data. These observations were consistent with previous studies demonstrating that European larch tends to maintain a relatively high transpiration rate during drought events, at least at high elevation (Badalotti *et al* 2000, Obojes *et al* 2018, 2020). This strategy appears the most efficient response for deciduous plants with a limited growing season, such as *L. decidua*. In order to compensate for a shorter growing period, European larch has twofold greater photosynthetic rates, a more carbon-efficient crown shape and canopy structure (Matyssek 1986, Gower and Richards 1990, Obojes *et al* 2018), and a higher stomatal conductance, compared to evergreen conifers that follow a water-saving strategy, such as *Picea abies*, *Pinus sylvestris* and *Abies alba* (Anfodillo *et al* 1998, Wieser 2012). Moreover, larch is a deep-rooting species and has shown osmotic adjustments facilitating water uptake in dry conditions (Badalotti *et al* 2000).

4.2. Are the larch responses in line with the responses observed at the ecosystem level?

Although the absence of a significant impact on the C-source process at the ecosystem level, a significant reduction (-17%) of stem growth and a contraction (-50%) of the growth period length occurred in 2017.

At the same time, in 2017 we observed not only the lowest growth but also the lowest values of tree water deficit, which was consistent with the essential role of water availability for turgor-driven cell division in the stem and for the regulation of carbon allocation. Tree water deficit is a valuable indirect measure for detecting physiological responses to water deficits (Zweifel *et al* 2005, Oberhuber *et al* 2015). During dry periods water stored in the sapwood can provide a small contribution to maintain a positive water balance in trees and thus can be significantly reduced (Bréda *et al* 2006).

Indeed water balance variables, such as climatic water deficit, may have the largest negative impact on inter-annual tree growth (Itter *et al* 2017) and limited stem growth was already observed in *L. decidua*, especially when drought events occurred during spring and early summer (Vitas 2018, Leštianska *et al* 2020, Danek *et al* 2021). Moreover, previous studies highlighted a strong dependence of tree growth to mean summer temperature in relation to elevation, with negative effects under 1300 m asl and positive responses at higher elevations (Vitasse *et al* 2019). According to these findings, we found that, in absence of limiting water availability, the warmer temperatures that occurred before budburst in 2015 did not determine any growth reduction or halt, and even

increased stem growth amount and duration. Therefore, we suggest that the 2017 early summer drought was the main driver of larch stem growth decrease at our study site (Oberhuber *et al* 2014, Jezik *et al* 2016, Leštianska *et al* 2020).

4.3. What is the relation between C-source (i.e. photosynthesis) and C-sink (i.e. tree stem growth) processes, during climate extremes?

The independence between carbon sequestration and tree growth (figures 5 and 6), proved by the observed decrease of stem radial increment in front of a constant GPP rate, implies two different hypotheses which do not exclude each other: (i) a shift in plant carbon allocation towards the prioritization of NSC storage within leaves and roots over growth processes (Sala *et al* 2012, Blessing *et al* 2015, Churakova *et al* 2016, Hartmann *et al* 2020), which question the C-source limitation hypothesis, usually applied in vegetation modeling (Fatichi *et al* 2014, 2019); (ii) the 'Insurance Hypothesis' (Yachi and Loreau 1999), which can be used to explain the stability of the ecosystem carbon sequestration, assuming that the negative effects of climatic fluctuations on larch growth might have been buffered by the asynchrony responses of the understory species.

By now, it is well known that NSC storage is not a passive overflow but an active sink regulated by trees, which during drought increase NSC storage at the expense of short-term growth to optimize growth and survival in the long term (Smith and Stitt 2007, Muller *et al* 2011, Blessing *et al* 2015). Indeed, the osmotically active and soluble fraction of NSCs is important to maintain cell turgor and vascular integrity (xylem and phloem), and may be involved in the sensing (Secchi and Zwieniecki 2011) and reversal of embolism (Nardini *et al* 2011). Moreover, tree growth may be limited by factors other than carbon supply by photosynthesis (Körner 2003), especially water availability that affects important growth-related processes such as turgor-driven cell expansion (Woodruff *et al* 2004).

A relevant outcome of our study, confirming the needs of future research on tree growth-climate sensitivities to improve model reliability, is that the stem growth reduction observed in 2017 was not the result of a stationary relationship between tree-level processes and climatic variability, but rather the result of a single-year event that occurred in a critical moment of the tree phenological development. This observation not only highlights the crucial role of the extreme timing (Sippel *et al* 2016, 2018b), but also supports the hypothesis of an intrinsic variability in growth sensitivity to climate (Peltier and Ogle 2020).

We are aware that cross-scale discrepancies, due to the different sampling scales of tree- vs. ecosystem-level measurements, represent the larger source of uncertainty in our work. However, we believe that

the nature of our system as well as the statistical distribution of our data properly support our findings. Indeed, the forest stand investigated in our study was homogeneous, and the sampled individuals well represented the tree population within the eddy flux footprint (see section 2.4). As regards the ecosystem fluxes, the well-known systematic errors that can affect the eddy covariance method (e.g. nighttime flux underestimation) may cause a bias in the observed absolute yearly cumulative value. Nevertheless, the uncertainties obtained considering different calculation methods (table 2) demonstrated that the systematic errors had a minor role in the flux interannual variability at the study site, which was the main focus of our investigation.

By combining tree- and ecosystem-based observations, we demonstrated that larch growth decrease was not driven by a reduction of the photosynthetic activity. This outcome corroborates recent criticisms of the C-source limitation paradigm applied in vegetation modelling, and it supports the idea that a direct causal link from carbon assimilation to plant growth may be an oversimplification (Fatichi *et al* 2014, 2019, Hartmann *et al* 2020, Eckes-Shephard *et al* 2021). Being aware of this theoretical framework is crucial for the development of vegetation models able to predict with increasing reliability forest responses to climatic fluctuations and the mitigation potential of these ecosystems. Indeed, according to our results, investigating tree- and ecosystem-level responses separately might lead to draw misleading conclusions on forest functioning: e.g. high sensitivity in terms of tree growth, and low sensitivity in terms of ecosystem carbon sequestration.

5. Conclusions

Our study provided evidence of the independence between C-source and C-sink process anomalies in a subalpine larch forest under heat and drought events. Indeed, the observed reduction of tree stem growth under drought conditions did not correspond to a reduction in the amount of carbon fixed through photosynthesis. Moreover, the evidence of a significant higher tree water deficit during the 2017 growing season highlighted the occurrence of European larch stress under the occurring heat and drought events.

On one side, the observation that tree growth reduction was not driven by a decrease in the photosynthetic activity suggests the rejection of the C-source limitation hypothesis, and make the revision of process-based vegetation models urgent, in order to increase the reliability of their projections and to avoid misleading conclusions driven by the analysis of a single ecosystem process and/or by the assumption of the ecosystem response stationarity.

On the other side, the occurrence of tree water stress even at high altitudes requires further investigations, especially for wet sites, where plant species have smaller safety hydraulic margins (Peters *et al* 2021). A future change in the spatial distribution of larch forests, driven by climate change and extreme events, may have negative effects not only on silvicultural use of this species but also on the ecosystem services provided by larch forests, especially at lower elevations in the European Alps.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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