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Physiological response of Swiss ecosystems to 2018 drought across plant types and elevation

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Using five eddy covariance flux sites (two forests and three grasslands), we investigated ecosystem physiological responses to the 2018 drought across elevational gradients in Switzerland. Flux measurements showed that at lower elevation sites (below 1000 m.a.s.l.; grassland and mixed forest) annual ecosystem productivity (GPP) declined by approximately 20% compared to the previous 2 years (2016 and 2017), which led to a reduced annual net ecosystem productivity (NEP). At the high elevation sites, however, GPP increased by approximately 14% and as a result NEP increased in the alpine and montane grasslands, but not in the subalpine coniferous forest. There, increased ecosystem respiration led to a reduced annual NEP, despite increased GPP and lengthening of the growing period. Among all ecosystems, the coniferous forest showed the most pronounced negative stomatal response to atmospheric dryness (i.e. vapour pressure deficit, VPD) that resulted in a decline in surface conductance and an increased water-use efficiency during drought. While increased temperature enhanced the water-use efficiency of both forests, de-coupling of GPP from evapotranspiration at the low-elevation grassland site negatively affected water-use efficiency due to non-stomatal reductions in photosynthesis. Our results show that hot droughts (such as in 2018) lead to different responses across plants types, and thus ecosystems. Particularly grasslands at lower elevations are the most vulnerable ecosystems to negative impacts of future drought in Switzerland.

This article is part of the theme issue 'Impacts of the 2018 severe drought and heatwave in Europe: from site to continental scale'.

1. Introduction

The summer of 2018 was among the most severe summer droughts ever recorded in Europe: remotely sensed vegetation indices show that in large parts of the continent, the 2018 drought even exceeded the hot drought of 2003, with hotspots identified mostly north of the Alps, including parts of Switzerland [1].

In Switzerland, 2018 included the fourth warmest spring (March, April, May) and the third warmest summer (June, July, August) since the start of the instrumental measurements in 1864 [2]. North of the Swiss Alps—where all our study sites are located—a 10-day long heatwave occurred between 30 July and 8 August, with daily maximum temperatures above 30°C [2]. While summer 2018 received only 70% of the long-term mean precipitation (1981–2010), snowfall was above normal in winter, and winter precipitation reached over 130% of its long-term mean [2].

Previous drought events have been shown to cause a significant decrease in agricultural yield and an increase in tree mortality [3–5]. Naturally, understanding the impact of extreme conditions on the functioning of ecosystems is fundamental to

reducing environmental as well as economic damage, and advancing the capacity to predict future responses to re-occurring extreme events [6]. In particular, regions that are typically not exposed to high temperatures (greater than 30°C) might be at a greater risk of damage to their ecosystem's functioning than those regions which experience such conditions regularly [7,8].

(a) Ecosystem physiological response to drought

Droughts and heatwaves impose multiple effects on plant functioning. At the ecosystem scale, the stomatal response is characterized through surface conductance (G_s), which plays an important role in regulating evapotranspiration and productivity [9]. When plants close their stomata in response to low soil water contents (SWC) and increased atmospheric vapour pressure deficit (VPD), CO_2 uptake is reduced and photosynthesis is impaired [10]. Stomatal closure also tightly regulates the carbon-water coupling, which is characterized most widely through plant water-use efficiency (WUE) [11,12], the response of which to climate change is not very well known for different plant types [13–15].

The link between photosynthesis and transpiration controls the flux of water and carbon dioxide in plants, and its notion is essential to many Earth system models [16–20]. While photosynthesis can be limited by stomatal conductance, it can also be limited by biochemical processes that are sensitive to increases in leaf temperature [21]. Such biochemical processes include the carboxylation of the Rubisco enzyme (ribulose-1, 5-bisphosphate) which is highly sensitive to changes in temperature in the leaf environment [22,23]. Understanding how different ecosystems respond physiologically to drought and provide feedback to the carbon and water cycle can reduce the uncertainties in future climate projections [24–26].

(b) Identification of drought

Drought is commonly identified as a set of conditions when lack of precipitation and increased temperatures manifest as deficits in soil moisture [27]. In this study, we used long-term measurements of atmospheric VPD and SWC at each site to identify periods when sites were exposed to unusually dry conditions. VPD was selected since it reflects the combined effect of air temperature and air humidity, and is known to directly affect plant water use (i.e. transpiration) and productivity (i.e. photosynthesis) and have a larger effect on plant physiological processes than precipitation or temperature *per se* [28,29]. Our objectives in this study were (i) to investigate how productivity was affected by the 2018 drought in high- versus low-elevation ecosystems, and (ii) to compare the physiological response of trees (coniferous and deciduous) versus grasses (C_3) to the combined soil and atmospheric dryness, across their elevational gradient. Elevation integrates many different climatological variables as well as management intensity for grassland studies. Switzerland is a suitable case study for testing these objectives because the elevational gradient spans a range of bioclimatic conditions, and therefore plant types and management intensities, within a relatively small geographical area.

2. Methods

(a) Site description

Study sites include two forests and three grasslands with continuous eddy covariance flux measurements across several

years (table 1). The sites are distributed over a range of elevations, from about 400 to 2000 m.a.s.l. Mean annual temperature across the sites varies from 2.3 to 9.5°C, and mean annual precipitation varies between 918 and 1651 mm (table 1). The study sites are part of the SwissFluxNet (www.swissfluxnet.ch), with one site being a Class 1 ICOS site (CH-DAV).

Vegetation in the subalpine coniferous forest (CH-DAV) consists of Norway spruce (*Picea abies* (L.) Karst) [39]. The overstorey vegetation in the mixed deciduous forest (CH-LAE) consists mainly of beech, ash, fir, spruce, lime, maple, oak and elm trees (*Fagus sylvatica* L., *Fraxinus excelsior* L., *Abies alba* Mill., *Picea abies* (L.) Karst., *Tilia cordata* Mill., *Acer pseudoplatanus* L., *Quercus robur* L. and *Ulmus glabra* Huds., respectively). Generally, the understory vegetation is scarce, consisting mainly of *Allium ursinum* L. flowering in early spring [40].

The pasture of the alpine grassland site (CH-AWS) is classified as *Deschampsia cespitosae*–*Poetum alpinae* community, with red fescue (*Festuca rubra*), Alpine cat's tail (*Phleum rhaeticum*), white clover (*Trifolium repens*) and dandelion (*Taraxacum officinale*) as dominant species. In the montane grassland site (CH-FRU), the species mixture consists of ryegrass (*Lolium* sp.), meadow foxtail (*Alopecurus pratensis*), cocksfoot grass (*Dactylis glomerata*), dandelion (*T. officinale*), buttercup (*Ranunculus* sp.) and white clover (*T. repens*), which cover up to 90% of the surface. Dominant vegetation for the low-elevation (Swiss plateau) grassland site (CH-CHA) is a mixture of Italian ryegrass (*L. multiflorum*) and white clover (*T. repens*), predominantly used for fodder production and occasional winter grazing by sheep [36]. For further description of the study sites, see table 1.

(b) Dataset

Eddy covariance fluxes were calculated using the free and open source software *EddyPro* (version 6, LI-COR) and then made available through the Drought 2018 Team as part of the ICOS Ecosystem Thematic Centre (ETC) dataset [41]. Post-processing, such as the gap-filling of flux variables, was done by the ICOS ETC and followed the FLUXNET data processing pipeline and naming convention (<https://fluxnet.fluxdata.org/data/fluxnet2015-dataset>). From this dataset, we selected a net ecosystem exchange (NEE) that was filtered with a variable friction velocity threshold (namely NEE_VUT_REF). Gross primary productivity (GPP) and ecosystem respiration (RECO) that were used in this study were partitioned based on Reichstein *et al.* [42]. For easier interpretation, the net annual balance of NEE is presented as net ecosystem productivity ($\text{NEP} = -\text{NEE}$).

(c) Atmospheric and soil dryness

To test if the conditions in 2018 were unusually dry at a site, we compared daily VPD in 2018 with the site-specific long-term median, excluding years that were recognized across Europe as extremely hot and dry years (i.e. 2003, 2010, 2015) [43]. The averaging period for the long-term median was dependent on the measurement period at each site (table 1).

At the daily timescale, we considered days drier than normal if VPD was above the long-term 90% quantile. We used a soil water deficit index (SWDI) [44] that is sensitive to soil texture and hydraulic properties (described below) to assess soil dryness based on SWC. Volumetric SWC was typically measured at several depths at each site—except at CH-AWS where measurements were available from one depth only. For the forest sites, we calculated the depth-weighted average SWC using data from each layer and depth of the layer, following the method of Gao *et al.* [45]:

$$\theta_p = \frac{2\theta_1 L_1 + (\theta_1 + \theta_2)L_2 + (\theta_2 + \theta_3)L_3 + (\theta_3 + \theta_4)L_4 + (\theta_4 + \theta_5)L_5}{2(L_1 + L_2 + L_3 + L_4 + L_5)}, \quad (2.1)$$

Table 1. Description of the five eddy covariance (EC) sites. Soil information for CH-AWS are from Hiller *et al.* [30], for CH-FRU and CH-CHA from Roth [31], and for CH-DAV and CH-LAE from Etzold *et al.* [32] and based on measurements collected by Lorenz Walthert at WSL. Soil texture type corresponds to the depth at which soil moisture is measured.

site	CH-DAV	CH-LAE	CH-AWS	CH-FRU	CH-CHA
land cover	subalpine coniferous forest	mixed deciduous forest	alpine grassland	montane grassland	low-elevation grassland
latitude	46° 48' 55" N	47° 28' 42" N	46° 34' 59" N	47° 06' 57" N	47° 12' 37" N
longitude	9° 51' 21" E	8° 21' 52" E	9° 47' 25" E	8° 32' 16" E	8° 24' 38" E
elevation (m.a.s.l.)	1639	682	1978	982	393
mean annual precipitation (mm)	1046	1211	918	1651	1136
mean annual temperature (°C)	3.5	8.7	2.3	7.2	9.5
soil type	Chromic cambisols Rustic podsols	Rendzic leptosols Haplic cambisols	Humous sandy loam	Gleysol	Cambisol
soil moisture depth (cm)	0–24	0–30	0–5	0–5	0–5
soil texture	sandy loam	clay loam	sandy loam	sandy loam	silty loam
field capacity (%)	18	36	18	18	31
permanent wilting point (%)	8	22	8	8	11
start of continuous EC measurements	January 1997	April 2004	May 2014	August 2005	July 2005
terrain slope	saddle position	24°	25°	<5°	flat
fetch	>200 m	>1 km	>120 m	>80 m	>130 m
reference	Etzold <i>et al.</i> [32]; Haeni <i>et al.</i> [33] ^a	Göckede <i>et al.</i> [34]; Etzold <i>et al.</i> [35]; Haeni <i>et al.</i> [33] ^a	Hiller <i>et al.</i> [30]; Zeeman <i>et al.</i> [36]; Hörtnagl <i>et al.</i> [37] ^a	Zeeman <i>et al.</i> [36]; Hörtnagl <i>et al.</i> [37] ^a	Zeeman <i>et al.</i> [36]; Fuchs <i>et al.</i> [38] ^a

^aThe corresponding reference for long-term mean precipitation and mean temperature values.

where θ_p refers to the profile SWC ($\text{m}^3 \text{m}^{-3}$); θ refers to SWC at the i th layer ($\text{m}^3 \text{m}^{-3}$) and L_i ($i = 1, 2, \dots, 5$) refers to the depth of the i th soil layer (m). In the grassland sites, a shallow root zone was considered and measurements from the top 5 cm were used in the analysis, while in the forests soil water measurements of up to 30 cm (available depth for both forest sites) were used. Daily SWDI was calculated using daily SWC, and site-specific soil physical properties (table 1) [44]:

$$\text{SWDI} = \left(\frac{\theta_p - \theta_{\text{FC}}}{\theta_{\text{AWC}}} \right) 10, \quad (2.2)$$

where θ_{FC} is soil moisture at field capacity (i.e. the upper limit of the available water for plants), and θ_{AWC} is the available water content (i.e. the difference between soil moisture at field capacity and soil moisture at the permanent wilting point, θ_{PWP}). SWDI is a fractional magnitude multiplied by ten to display a range of meaningful values, in terms of soil water availability. When SWDI is above zero, the soils have excess water; when it equals zero, the soil is at the field capacity of water content (i.e. no water deficit), and when the SWDI reaches ≤ -10 water deficit is absolute (wilting point) [44,46]. Soil water characteristics (e.g. field capacity and PWP) were derived for each soil texture type from Saxton *et al.* [47].

In order to test plant physiological responses over a wider range of conditions, we used the available range of VPD and SWDI at each site to separate high/low dryness conditions. We

considered the top 25% quantile of SWDI as low, and the lower 25% as high soil dryness. In terms of atmospheric dryness, we considered the top 25% VPD quantile as high, and the lower 25% of VPD as low atmospheric dryness.

(d) Growing period

For the analysis of the physiological responses, we focused on the growing period, specific to each site. At the forest sites, the start and end of the growing period was identified from dendrometer records following the method of Zweifel *et al.* [48]. For the grassland sites, growing period was considered equal to the net carbon uptake period (CUP). The start of the CUP was defined as the date when the 10-day daily moving average NEE turned to net uptake ($\text{NEE} < 0 \mu\text{mol m}^{-2} \text{s}^{-1}$), and the end of the growing period was identified when this condition no longer held (adapted from Wohlfahrt *et al.* [49]). At the grasslands sites, if moving average NEE turned to net CO_2 emission for a few days in spring/summer, but resumed again to net CO_2 uptake (e.g. due to management), we considered the growing period to continue until autumn depending on daily NEE fluxes.

(e) Physiological variables

At the ecosystem level, plant stomatal response is reflected in surface conductance (G_s).

Figure 1. Atmospheric and soil dryness in 2018 across the study sites. VPD above the long-term 90% quantile shows periods of unusually dry air. Soil water deficit index (SWDI) below zero indicates limited water available to plants. In CH-LAE (b), complete soil water content measurements were available until 20 November 2018 only.

We calculated G_s (m s^{-1}) by inverting the Penman–Monteith equation [50]

$$\frac{1}{G_s} = r_s = \frac{\{e_s(T) - e\} \rho_a c_p}{\lambda E (\Delta + \gamma) - \Delta H} - r_a, \quad (2.3)$$

where r_s and r_a are surface and bulk aerodynamic resistances, respectively (s m^{-1}), $e_s(T)$ is saturation vapour pressure (kPa) at temperature T ($^{\circ}\text{C}$), e is actual vapour pressure (kPa), ρ is the dry air density (kg m^{-3}), c_p is the specific heat capacity of air ($\text{J kg}^{-1} \text{K}^{-1}$), λE is the latent heat flux (LE, W m^{-2}), Δ is the slope of the saturation vapour pressure curve (kPa K^{-1}) at a given temperature, γ is the psychrometric constant (kPa K^{-1}), and H is the sensible heat flux (W m^{-2}). Bulk aerodynamic resistance r_a was calculated based on the relationship between horizontal wind speed (U , m s^{-1}) and friction velocity (u_* , m s^{-1}) [51]

$$r_a = \frac{U}{u_*^2} + 6.2u_*^{-0.67}. \quad (2.4)$$

Surface conductance combines conductance from the canopy (G_c) with evaporation from the soil and from the water intercepted by the canopy. G_s is thus physiologically meaningful only during periods when vegetation is active, and evaporation from vegetation and soil surfaces is minimum ($G_s \approx G_c$) [52]. In order to minimize the effect of evaporation on G_s after rainfall, we removed data immediately following rainfall with the following criteria: if precipitation exceeded 0.5 mm during the last 12 h, 1 mm during the last 24 h, or 2 mm during the last 2 days [53]. Surface conductance was calculated from measured half-hourly fluxes and outliers were removed following the method described in Rogiers *et al.* [54], where a running mean was calculated over one month and all values larger or smaller than three times the running standard deviation were removed. In this study, evapotranspiration (ET) is presented either in energy unit (W m^{-2}) based on latent heat measurements, or in millimetre of water.

We tested the stomatal response at different ecosystems based on the response of surface conductance to VPD, under dry and wet soil conditions [29,55]. Sensitivity of stomata to

VPD, which is an indicator of vegetation water-use strategy, is often characterized with parameter m , the slope of G_s (assuming $G_s \approx G_c$) response to $\log_e(\text{VPD})$ [55]

$$G_s = m \ln \text{VPD} + b. \quad (2.5)$$

In addition, we addressed the coupling between ET and GPP under two main dryness conditions: wet air and wet soil versus dry air and dry soil, on the notion that if stomatal regulation is strong, reductions in GPP will be accompanied by reduction in ET [56].

We used underlying water-use efficiency ($\text{WUE}_u = \text{GPP} \cdot \text{VPD}^{0.5} / \text{ET}$) to compare the ratio of carbon gain to water loss [12]. WUE_u is physiologically more meaningful than ecosystem WUE (GPP / ET) and is a preferred method to ecosystem intrinsic WUE ($\text{WUE}_i = \text{GPP} \cdot \text{VPD} / \text{ET}$) as it incorporates the non-linear effect of VPD on plant carbon–water relations [12,52,57,58]. An analysis of covariance (ANCOVA) was used to compare the slope of a linear regression between $\text{GPP} \cdot \text{VPD}^{0.5}$ and ET.

3. Results

(a) Atmospheric and soil dryness across the study sites

The year 2018 was a dry year across the Swiss sites, except for the alpine grassland site (CH-AWS) (figure 1). Rainfall declined in 2018, and air temperature increased compared to the previous 2 years 2016 and 2017 (table 2; electronic supplementary material, figure S3). In winter 2018 (January–March) VPD was below the long-term average at all sites (figure 1). Atmospheric and soil dryness were most aligned at the low-elevation grassland site (CH-CHA, figure 1), presumably due to the low contribution of snow to SWC, and among all sites, atmospheric drought was most severe here (CH-CHA). The lower elevation forest site (CH-LAE) was continuously water-limited in the top 30 cm of the soil (in terms of plant available water) in 2018, while the alpine

Table 2. Anomalies in total annual precipitation (P), mean annual air temperature (T), mean annual volumetric soil water content (SWC), total annual potential evapotranspiration (ET_0) [59], total annual actual evapotranspiration (ET), total annual latent heat flux (LE), total annual sensible heat flux (H), total annual gross primary productivity (GPP), total annual ecosystem respiration (RECO) and annual net ecosystem productivity (NEP or -NEE) in 2018 compared to the 2016–2017 mean. Note that total annual sums were derived from gap-filled fluxes.

site	ΔP (mm)	ΔT (°C)	ΔSWC (%)	ΔET_0 (mm)	ΔET (mm)	ΔLE (MJ m ⁻²)	ΔH (MJ m ⁻²)	ΔGPP (g C m ⁻²)	$\Delta RECO$ (g C m ⁻²)	ΔNEP (g C m ⁻²)
CH-DAV	−657	+0.8	−4	+67	−12	−32	+110	+117	+133	−111
CH-LAE	−41	+0.9	−1	+73	−196	−485	+62	−301	+40	−380
CH-AWS	+25	+0.6	+14	+8	−71	−176	−87	+183	+102	+101
CH-FRU	−445	+0.7	−2	+22	+74	+181	+84	+403	+346	+170
CH-CHA	−343	+1.02	−5	+83	−63	−156	+144	−708	−606	−35

Table 3. Start and length of the growing period at each site. In forests (CH-DAV and CH-LAE), the growing period was measured with point dendrometers. The growing (i.e. net carbon uptake) period in grasslands was defined as the period when the 10-day daily moving average NEE indicated net uptake ($NEE < 0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

site	start of growing period (day of year)			length of growing period (no. of days)		
	2016	2017	2018	2016	2017	2018
CH-DAV (<i>dendrometers</i>)	167	148	152	91	76	121
CH-LAE (<i>dendrometers</i>)	127	125	121	91	124	161
CH-AWS	118	106	117	191	193	182
CH-FRU	93	78	75	166	196	233
CH-CHA	41	78	35	257	196	264

and montane grasslands (CH-AWS and CH-FRU) had sufficient soil water supply throughout the year (figure 1). It is important to mention, however, that soil moisture measurements in shallower depths are difficult to interpret at high elevation sites during winter, due to frozen soil conditions.

(b) Gross primary productivity and ecosystem respiration responses

Warmer and drier conditions in 2018 reduced annual GPP at the mixed forest and the lowland grassland (CH-LAE, CH-CHA), but increased GPP at the alpine and montane sites (CH-DAV, CH-AWS, CH-FRU) (table 2; electronic supplementary material, figure S1). Apart from the low-elevation grassland site (CH-CHA), ecosystem respiration increased relative to previous years at all sites (table 2; electronic supplementary material, figure S1).

On average, the growing period measured with point dendrometers was about one month longer for the mixed deciduous forest (CH-LAE) than for the subalpine coniferous forest (table 3). In 2018, growing period increased by 53 days at the mixed forest (CH-LAE) and by 37 days at the coniferous forest (CH-DAV) compared to the previous years (2016–2017) (table 3).

(c) Light-use efficiency response to atmospheric and soil dryness

Across all ecosystems, light-use efficiency—defined as the initial slope of the light response curve—declined with increase in VPD or soil dryness (electronic supplementary material, figure S2 and table S1). In forests, light-use efficiency and reference

GPP (GPP at saturating light) responded more to atmospheric dryness than to soil dryness. Increased temperatures reduced net CO_2 uptake more substantially at the low-elevation grassland (CH-CHA) than at the mixed forest site (CH-LAE) (figure 2). At the high-elevation sites, temperature increased CO_2 uptake most in the montane grassland site (CH-FRU).

(d) Ecosystem stomatal response to atmospheric and soil dryness

Between the two forest sites, sensitivity of stomata to changes in the atmospheric VPD (reflected in G_s) was stronger in the subalpine coniferous forest (CH-DAV) than in the mixed deciduous forest (CH-LAE) and regardless of SWC, surface conductance declined with increasing VPD (figure 3). Larger stomata sensitivity to VPD in the coniferous forest was characterized by a larger parameter m (0.05 ± 0.01 standard error of the mean, equation (2.5), figure 3) compared to the deciduous forest (0.03 ± 0.01 se of the mean) under dry soil conditions. In response to a dry period in summer (mid-July to mid-August 2018; figure 1) and in spring (mid-April to mid-May 2018) water-use efficiency increased in forests (particularly in spring) but declined or remained unchanged at the grassland sites (figure 4).

4. Discussion

(a) Effect of drought on gross primary productivity

Drought in 2018 reduced GPP in the mixed deciduous forest and at the low-elevation grassland site by on average 20%,

Figure 2. Net ecosystem exchange (NEE) response to air temperature (T) under high (lowest 25% quantile SWDI) and low (highest 25% quantile SWDI) soil dryness. Data were binned by T with an equal number of observations in each bin. Symbols mark the median values and error bars show the 5–95% percentile range of the data in each bin. Data were pooled for 2016–2018, during the growing period only, measured only, and daytime only (global radiation $> 0 \text{ W m}^{-2}$).

Figure 3. Surface conductance (G_s) response to VPD under high (lowest 25% quantile of SWDI) and low (highest 25% quantile of SWDI) soil dryness. Data were limited to rain-free conditions as defined in §2e, within the growing period, and under peak light conditions (when PPFD $> 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$). Only measured fluxes were used. Data were pooled for 2016–2018. Symbols show the upper (75%) quantile of VPD and G_s in each bin, and error bars mark the mean to maximum range of G_s . Negative relationship between G_s and VPD under dry soil was significant ($p < 0.05$) for CH-DAV, CH-LAE and CH-CHA.

but had a positive effect on the productivity of the alpine, subalpine and montane sites (on average 14% increase), even during driest conditions (table 2, electronic

supplementary material, figure S1). The sites where GPP (and as a result NEP) was negatively affected in 2018 (CH-LAE, CH-CHA) were those that are generally warmer

Figure 4. Underlying water-use efficiency (i.e. relationship between $GPP \cdot VPD^{0.5}$ and ET) during two different periods of limited water availability, in spring (15 April–15 May) and in summer (15 July–15 August) 2018 compared to the same period in 2017.

Figure 5. Diel coupling of GPP with LE (i.e. evapotranspiration in $W m^{-2}$) during dry and wet conditions. Dry air is defined by VPD above the long-term 90% quantile, and dry soil is defined by SWDI in the lowest 25% quantile. Data were averaged over all days when the wetness conditions were met. Error bars are standard errors of the mean for each hour. Arrows mark the direction of change in GPP with time of day.

and drier (figure 1; electronic supplementary material, figure S3). In the mixed deciduous forest (CH-LAE), soil moisture was continuously limiting in the top 30 cm in 2018—although previous stable isotope measurements of root water uptake showed that at this site, the source of water for trees can be from 70 cm depth [60]. Higher respiration seemingly stimulated by higher temperatures [61,62] reduced NEP in the subalpine coniferous forest, despite increased GPP and lengthening of the growing period.

(b) Effect on surface conductance of water vapour

In grasslands, G_s did not decrease with VPD in the alpine site (figure 3). Here surface evaporation (of water intercepted by dense grass cover) might have masked the response of stomata to VPD, even though we removed data after rainfall to minimize its effect [63]. At the alpine site, SWC was more than average in 2018 despite less precipitation inputs (figure 1 and table 2). Comparison of SWC with river discharge measurements from a nearby station (1 km away) showed a substantial increase in runoff in 2018 (data not

shown). This suggests that the observed soil moisture could be the result of a colder than usual winter, deeper snow pack, warmer than usual spring temperatures, and increased water from snowmelt in 2018 at the alpine grassland site.

(c) Effect on underlying water-use efficiency

In the subalpine coniferous forest, GPP increased with warmer temperatures and coincided with reduced ET (due to strong stomatal regulation) (figure 3), which improved WUE_u compared to the previous year (figure 4). Typically, as VPD increases, stomatal conductance decreases, and if photosynthesis is not negatively affected, WUE_u increases [12,64]. However, under extreme conditions, productivity can get compromised through a reversible deactivation of the photosynthetic system [65]. Therefore, GPP can mask the effect of reduced G_s on water-use efficiency [66] and WUE_u can remain unchanged or even decline [67,68].

In forests, stomatal regulation seems to be a strong factor controlling the carbon–water relations, whereas in grasslands, there seems to be a de-coupling between assimilation

and transpiration during dry conditions, due to the lack of strong stomatal regulation [56]. Immediately after sunrise, GPP increases with light and inevitably also evapotranspiration (figure 5, ET shown here in energy units, LE). In the afternoon and with decreasing light, both GPP and ET start to decline. Under dry conditions, however, at the low-elevation grassland site (CH-CHA), where productivity was most affected, assimilation started to decline during the day while ET continued increasing (in average for up to 5 h), an indication that reduction in GPP was not due to a reduced stomatal conductance, but rather due to a temperature-induced downregulation of GPP [65,69]. This mechanism, which was evident at the sub-daily timescale, controls differences in WUE between trees and grasses under drier conditions (e.g. increase in WUE of forests versus decrease or no change in grasslands) [70,71].

Summer of 2018 was exceptionally dry in Switzerland, but the extent of drought was not uniform across all sites, and decreased with elevation. GPP declined at lower elevation sites, while sites above 1000 m.a.s.l. were positively affected. There, both grasslands and forests profited, because precipitation in normal years tends to be in surplus of plant and atmospheric demand, and temperatures are below the plant physiological growth optimum, so that a drought period similar to 2018 brings high elevation sites closer towards optimum growth conditions [72,73]. By contrast, conditions at lower elevation sites shifted away from such an optimum, towards too warm and too dry [73].

Mountain ranges in general are orographic barriers that tend to lift the advected air, which leads to orographic precipitation [74,75] that is still available during drought years, although less abundant than in normal years. During summer, thunderstorms and shower cells tend to travel along orographic structures, in Switzerland along the Alps [76]. The higher water holding capacity of air at warmer temperatures is not only expected to be responsible for differences in rainfall at higher elevations as compared to lower ones, but it might even lead to increased summer precipitation under climate warming [77]. Thus, findings from 2018

presented here are expected to give strong evidence that higher elevation ecosystems will increase, not decrease, productivity under dryer and warmer conditions, whereas at lower elevations the effect on GPP and NEP is clearly negative.

5. Conclusion

Droughts can have contrasting effects on plant physiology and ecosystem productivity in mountainous regions: while lower elevation sites will experience reduced plant productivity, plants at elevations above 1000 m.a.s.l. can profit from drier conditions. The net effect on the ecosystem capacity for CO₂ uptake will however depend on the response of respiration, which can compensate the increased productivity and reduce NEP even in the high elevation sites despite warming and lengthening of the growing period (such as in the subalpine coniferous forest in this study). Studies that aim to make realistic projections of future climate need improved understanding of how different ecosystems respond to drought and how such response provides feedback to the global carbon and water cycles.

Data accessibility. DOI of the dataset used in this study is: doi:10.18160/yvr0-4898.

Authors' contributions. M.G., L.H., S.G., S.B., W.E. and N.B. conceived the study. M.G., L.H., E.P.L., S.G., I.F., K.M., S.E. and R.Z. generated data and M.G. and K.M. performed the analysis. All authors contributed to the interpretation and discussion of the results and contributed to the final manuscript.

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