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Contrasting response of grassland versus forest carbon and water fluxes to spring drought in Switzerland

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Abstract
Since the European summer heat wave of 2003, considerable attention has been paid to the impacts of exceptional weather events on terrestrial ecosystems. While our understanding of the effects of summer drought on ecosystem carbon and water vapour fluxes has recently advanced, the effects of spring drought remain unclear. In Switzerland, spring 2011 (March–May) was the warmest and among the driest since the beginning of meteorological measurements. This study synthesizes Swiss FluxNet data from three grassland and two forest ecosystems to investigate the effects of this spring drought. Across all sites, spring phenological development was 11 days earlier in 2011 compared to the mean of 2000–2011. Soil moisture related reductions of gross primary productivity (GPP) were found at the lowland grassland sites, where productivity did not recover following grass cuts. In contrast, spring GPP was enhanced at the montane grassland and both forests (mixed deciduous and evergreen). Evapotranspiration (ET) was reduced in forests, which also substantially increased their water-use efficiency (WUE) during spring drought, but not in grasslands. These contrasting responses to spring drought of grasslands compared to forests reflect different adaptive strategies between vegetation types, highly relevant to biosphere–atmosphere feedbacks in the climate system.

Keywords: Swiss FluxNet, drought response, eddy covariance, carbon dioxide fluxes, water vapour fluxes, water deficit, evapotranspiration, water-use efficiency

1. Introduction

Europe has experienced a number of exceptional weather events during the past decades that have attracted the interest of ecologists, such as severe droughts and heatwaves in summer 2003 (Ciais *et al* 2005) and 2010 (Barriopedro *et al* 2011), flood events in 2002 (Christensen and Christensen 2003) and 2005 (Schmocker-Fackel and Naef 2010), and severe storms—such as 'Lothar' in 1999 and 'Gudrun' in 2005 (Lindroth *et al* 2009). These events have claimed lives, caused substantial economic damage in agriculture, forestry and infrastructure, and heavily disturbed the carbon and water balances of terrestrial ecosystems in Europe (Ciais *et al*

2005, Reichstein *et al* 2007). With increasing atmospheric greenhouse gas concentrations, regional climate scenarios have predicted more intense and frequent extreme events in Europe for the future (Schär *et al* 2004, Frei *et al* 2006). In addition, soil moisture feedbacks to the atmosphere might further enhance extreme temperatures on local and regional scales due to reduced evaporative cooling (Granier *et al* 2007, Seneviratne *et al* 2010). However, our knowledge about the changes in ecosystem carbon and water fluxes in response to such extreme events is still limited, in particular during the transitional seasons of spring and autumn (Richardson *et al* 2010, Zhang *et al* 2012).

Research has recently focused on summer droughts and heatwaves, e.g. 2003 (Ciais *et al* 2005) and 2010 (Barriopedro *et al* 2011) in Europe. However, drought events have also occurred during spring, such as in France and south-eastern UK in 2006, in Germany, The Netherlands and Austria in April 2007, and more recently throughout most of central and north-western Europe in spring 2011 (Vogt 2012, Quesada *et al* 2012, Sepulcre-Canto *et al* 2012), when historic records of high temperatures were observed (European Drought Observatory 2011).

In Switzerland, spring 2011 was the warmest (+3.4 °C above average) and the third driest (−47% below average seasonal precipitation) since the beginning of meteorological measurements in 1864 (MeteoSwiss 2012), following an exceptionally dry winter with below average precipitation and snow accumulation (Pielmeier 2011). This combination resulted in a pronounced spring drought that affected plant phenology, agricultural production and water supply. Reservoir levels reached record lows, and irrigation measures were required to preserve agricultural production in parts of Switzerland (BAFU 2011).

The current understanding of drought effects suggests that plant water limitations are less likely in spring than in summer as soil reservoirs should have been recharged by winter precipitation. However, extreme weather events during early season growth could have severe effects on carbon and water fluxes of terrestrial ecosystems.

Only a few studies have investigated the effects of spring drought on ecosystem carbon and water fluxes so far. These studies reported overall reductions in carbon uptake (Zhang *et al* 2012, Dong *et al* 2011, Kwon *et al* 2008, Parton *et al* 2012), a small suppression in evapotranspiration (ET; Dong *et al* 2011), and a shift in the environmental controls of net ecosystem exchange (NEE) from vapour pressure deficit (VPD) to soil moisture with progressing drought (Kwon *et al* 2008). While the temperature effects are well understood, the effects of moisture limitation during spring on phenology, carbon uptake and water vapour fluxes remain unknown.

The objectives of our study are (1) to synthesize ecosystem carbon dioxide and water vapour fluxes from the national eddy covariance network, Swiss FluxNet, (2) to evaluate the phenological development of vegetation, (3) to investigate carbon–water interactions, and (4) to compare the response of grasslands and forests to the 2011 spring drought in Switzerland.

2. Material and methods

2.1. Swiss FluxNet

We synthesized data from the Swiss FluxNet national eddy covariance network (www.swissfluxnet.ch). Swiss FluxNet includes the major land-use types of deciduous and evergreen forests, grassland and cropland along an elevational gradient in Switzerland and currently encompasses eight long-term ecosystem sites. Our synthesis study included five of these sites that provided data for spring 2010 and 2011: Chamau, Oensingen1, Früebüel (managed grasslands, elevation range from 393 to 982 m a.s.l.), Laegeren (lowland mixed deciduous forest), and Davos (subalpine evergreen forest, table 1). All sites have a temperate climate with elevation as a confounding factor, particularly the montane grassland in Früebüel and the subalpine evergreen forest in Davos. Management varied across sites and included 4–6 grass cuts per year with subsequent manure or synthetic fertilizer applications in the intensively managed Oensingen1 and Chamau grasslands. At the moderately managed grassland Früebüel, only solid manure was applied once per year and grass cuts were occasionally replaced by cattle grazing. The Laegeren and Davos forest sites had no management events during the time of observations.

2.2. Flux measurements and data processing

Flux densities of carbon dioxide, water vapour and energy were measured during 2010 and 2011 using the eddy covariance (EC) method. The micrometeorological measurement setup consisted of open-path infrared gas analysers (Li-7500, LI-COR, Lincoln, USA) and three-dimensional sonic anemometers (models Solent R3-50 and HS, Gill Instruments, Lymington, UK). Raw data were recorded at 10 or 20 Hz and processed to half-hourly averages using the *eth-flux* EC software (Mauder *et al* 2008) or a comparable custom-made EC software for Oensingen1 (Ammann *et al* 2007). Post-processing included corrections for damping losses (Eugster and Senn 1995), air density fluctuations (Webb *et al* 1980), and data screening for optical sensor contamination, stationarity (Foken and Wichura 1996), low turbulence conditions (see table 1 for site-specific u_*-thresholds) and statistical outliers (14 day running mean with ±3 SD range). In addition, negative nighttime fluxes (unreasonable as no photosynthesis occurs at night) and a corresponding amount of positive nighttime fluxes were removed using a trimmed mean approach to avoid a systematic bias of cumulative sums. Standardized gap filling and partitioning of carbon dioxide fluxes was performed using the methodology by Reichstein *et al* (2005), i.e., with the marginal distribution sampling (MDS) gap filling algorithm and flux partitioning based on a temperature regression with nighttime fluxes ($\mathrm{GPP} = -\mathrm{NEE}_{\mathrm{daytime}} + \mathrm{TER}$). In addition, we corrected for physiologically unrealistic, negative values of gross primary productivity (GPP) when net ecosystem exchange (NEE) exceeded nighttime derived total ecosystem respiration (TER; e.g., with onset of turbulent mixing or following rainfall),

Table 1. Swiss FluxNet sites used in this synthesis study. Abbreviations denote the International Geosphere–Biosphere Programme (IGBP), mean annual temperature (MAT), mean annual precipitation (MAP), and friction velocity (u_*)—a measure for turbulence conditions. Data were compiled from published literature except MAP, which was derived from long-term data provided by MeteoSwiss (see table 2).

Site	Chamau	Oensingen1	Früebüel	Laegeren	Davos
IGBP land use, Abbreviation	Grasslands, GRA (intensively managed)	Grasslands, GRA (intensively managed)	Grasslands, GRA (moderately managed)	Mixed Forest, MF (deciduous dominated)	Evergreen Needleleaf Forest, ENF
Dominant species	Italian ryegrass (*Lolium multifl.*) White clover (*Trifolium repens*)	English ryegrass (*Lolium perenne*) Meadow foxtail (*Alopecurus prat.*) White clover (*Trifolium repens*)	Meadow foxtail (*Alopecurus prat.*) Cocksfoot grass (*Dactylis glomerata*) Dandelion (*Taraxacum offic.*) Buttercup (*Ranunculus sp.*) White clover (*Trifolium repens*)	European beech (*Fagus sylvatica*) Norway spruce (*Picea abies*) European ash (*Fraxinus excelsior*) Sycamore maple (*Acer pseudopl.*)	Norway spruce (*Picea abies*)
Latitude	47°12′36.8″N	47°17′08.1″N	47°06′57.0″N	47°28′42.0″N	46°48′55.2″N
Longitude	8°24′37.6″E	7°43′55.9″E	8°32′16.0″E	8°21′51.8″E	9°51′21.3″E
Elevation (a.s.l.)	393 m	452 m	982 m	682 m	1639 m
MAT	9.8 °C[a]	9.5 °C	7.5 °C[a]	7.4 °C	3.4 °C
MAP	1125 mm	1184 mm	1516 mm	1070 mm	992 mm
u_*-threshold ($\mathrm{m\ s^{-1}}$)	0.08	0.10	0.08	0.30	0.20
References	Zeeman *et al* (2009) Zeeman *et al* (2010)	Ammann *et al* (2007) Ammann *et al* (2009)	Zeeman *et al* (2009) Zeeman *et al* (2010)	Ahrends *et al* (2009) Zweifel *et al* (2010) Etzold *et al* (2010) Etzold *et al* (2011)	Zweifel *et al* (2010) Etzold *et al* (2011)

[a] Mean from 2006 to 2007 (Zeeman *et al* 2010).

by replacing TER with NEE and setting GPP to zero (Wolf *et al* 2011).

Besides flux densities, meteorological variables such as air temperature, relative humidity, precipitation, incoming shortwave radiation (R_G), soil temperature and volumetric soil water content (SWC, in %, 5 cm depth; except at Oensingen1: 10 cm) were measured continuously (half-hourly averages, sums for precipitation) at all sites. SWC was also measured at 15–30 cm depth but showed similar results as for 5 cm depth (not shown). Long-term precipitation data for nearby reference stations (see table 2) were provided by MeteoSwiss.

2.3. Phenology

Phenological development of vegetation was analysed from species-specific observational data (i.e., dates of phenological phases) provided by MeteoSwiss from the national phenological monitoring network. We used the following nearby stations from this network (including distance and direction from the respective tower site): Chamau–Muri (9.0 km, 317°NW), Oensingen–Wynau (6.6 km, 115°SE), Früebüel–Edlibach (7.5 km, 18°N), Laegeren–Oberehrendingen (5.7 km, 274°W), and Davos–Davos-Dorf (1.4 km, 244°SW). According to the composition of the dominant vegetation at each site (see table 1), we used the date of needle emergence of Norway spruce (*Picea abies*) for the Davos site, and averaged the dates of leaf unfolding of European beech (*Fagus sylvatica*) and needle emergence for Norway spruce (*Picea abies*) at the Laegeren site. For all grassland sites, we consistently used the same plant species and averaged the dates of full flowering from cocksfoot grass (*Dactylis glomerata*) and dandelion (*Taraxacum officinale*).

2.4. General conventions

We used the R statistics software package, version 2.13.2 (R Development Core Team 2009, www.r-project.org) for data analyses. Daytime data were defined by R_G exceeding 10 W $\mathrm{m^{-2}}$. The term ‘spring’ refers to the meteorological definition (March, April and May). We use the term ‘drought’ related to precipitation deficits, which can impose (1) plant physiological stress due to soil moisture deficiency and (2) stomatal adjustments in response to high VPD. We compare our data of 2011 relative to 2010, with 2011 being closer to the long-term average precipitation regime for most sites (see table 2).

3. Results

3.1. Weather conditions during spring 2011

The weather anomaly during spring 2011 resulted in record high temperatures (+3.4 °C above average) and substantial below average precipitation (−47%) in Switzerland (MeteoSwiss 2012). March and April were particularly dry and all sites received below average precipitation, ranging from −35 to −85% in March and −42 to −79% in April. The Früebüel montane grassland had the lowest deviations from the long-term mean (−35% and −42%), because of its topographic exposure. Most sites also received below

Table 2. Precipitation sums and relative deviations from the long-term means (1981–2010) for the year 2011. Deviations for 2010 are reported for comparison. Long-term data were derived from nearby reference stations by MeteoSwiss while data for 2010 and 2011 were measured directly at the sites.

Site	Chamau	Oensingen	Früebüel	Laegeren	Davos
Reference station	Cham	Wynau	Zugerberg	Dietikon	Davos
Mean ± SD (mm)					
Winter (DJF)	180 ± 70	251 ± 82	215 ± 100	238 ± 71	185 ± 82
Spring (MAM)	274 ± 85	264 ± 100	353 ± 111	279 ± 102	204 ± 56
Annual	1112 ± 162	1129 ± 201	1457 ± 272	1110 ± 164	1035 ± 156
2011 (mm)					
Winter (DJF)	165	173	245	132	66
Spring (MAM)	182	93	353	89	133
Annual	1084	995	869	624	776
Deviation 2011 (%)					
Winter (DJF)	−8	−31	+14	−45	−64
Spring (MAM)	−34	−65	0	−68	−35
Annual	−3	−12	−40	−44	−25
Deviation 2010 (%)					
Winter (DJF)	−5	−24	+23	−43	−56
Spring (MAM)	0	−34	+43	−29	−14
Annual	+3	−20	+58	−20	−28

average precipitation during early May 2011, but heavy precipitation events after DOY 131 (May 11) resulted in a substantial monthly surplus at Davos and Früebüel, and a small surplus in Chamau. During spring 2011, all sites except Früebüel had a cumulative precipitation deficit of 34–68% (mean 51%, Früebüel excluded), which was larger than the small deficit of 7% across all sites during spring 2010 (table 2). In both years, spring was preceded by similarly dry winters across sites, except at Früebüel (2010: −32%, 2011: −37%).

This precipitation anomaly during spring 2011 was also reflected in the temporal patterns of SWC (figure 1), with a substantial decrease from a maximum of 52% (overall mean) on DOY 95 (April 5) to a minimum of 30% on DOY 131 (May 11), which confined the spring drought across all sites between DOY 102–132 (April 12–May 12). Low and increasing SWC at the subalpine Davos site (1639 m) during March was related to frozen soil and associated measurement limitations. During spring 2011, all sites received higher amounts of daily R_{G} compared to 2010, in the range of +17% (Davos) to +36% (Früebüel), with a mean of +27% (data not shown). Daily VPD was substantially higher at all sites (overall mean +85%) during spring 2011, particularly at the forest sites (+228% *versus* +45% at grasslands). Spring was also substantially warmer in 2011 compared to 2010 (see figure 5), with mean air temperatures differences of +2.1 to +3.4 °C at our sites (overall mean +2.8 °C) and the largest increase found at the forest sites (+3.3 °C).

3.2. Phenological development

Phenological observations showed that vegetation development started 8–17 days earlier (overall mean −11 days) in 2011 compared to the mean of 2000–2011 (figure 2). The opposite pattern was observed in 2010, when vegetation started later at all sites (overall mean +7 days). While sites differed considerably between 2000 and 2009, the late vegetation developments in 2010 and the early vegetation development in 2011 were more consistent across all sites. Compared to 2010, spring phenology developed on average 18 days earlier during spring 2011 at our sites.

3.3. Range and magnitude of carbon and water vapour fluxes

We observed large differences in GPP and TER among sites during spring 2011 (figure 3, table 3). GPP was highest for the grassland sites Chamau (10.2 ± 4.5 $\mathrm{g\ C\ m^{-2}\ d^{-1}}$, mean ± standard deviation) and Früebüel (8.8 ± 5.3 $\mathrm{g\ C\ m^{-2}\ d^{-1}}$), while lowest GPP was found at the evergreen forest site in Davos (3.4 ± 1.9 $\mathrm{g\ C\ m^{-2}\ d^{-1}}$). During the drought period 2011 (DOY 102–132), GPP decreased substantially at Chamau (figure 3(a)). Smaller reductions in GPP were observed for the two other grassland sites Oensingen1 and Früebüel at the beginning and towards the end of the drought period (figures 3(b) and (c)). We did not find drought related GPP reductions of the forests. However, GPP of the two forest sites was substantially higher in 2011 compared to 2010 (LAE: +54%, DAV: +19%), while the grassland sites did not show a consistent pattern and substantially higher GPP was only found at Früebüel (+38%, table 3).

Range and magnitude of TER largely followed the GPP pattern, except for the forest sites Laegeren (3.4 ± 1.2 $\mathrm{g\ C\ m^{-2}\ d^{-1}}$) and Davos (1.5 ± 0.5 $\mathrm{g\ C\ m^{-2}\ d^{-1}}$), where TER remained low, remarkably stable and decoupled from GPP following the onset of drought conditions in April (figure 3). Management of the grassland sites (grass cuts and grazing) resulted in a short-term decoupling of TER from GPP, i.e., reduced GPP along with increased TER (figures 3(a)–(c)). Compared to 2010, we observed higher respiratory fluxes for the forest sites (LAE: +23%,

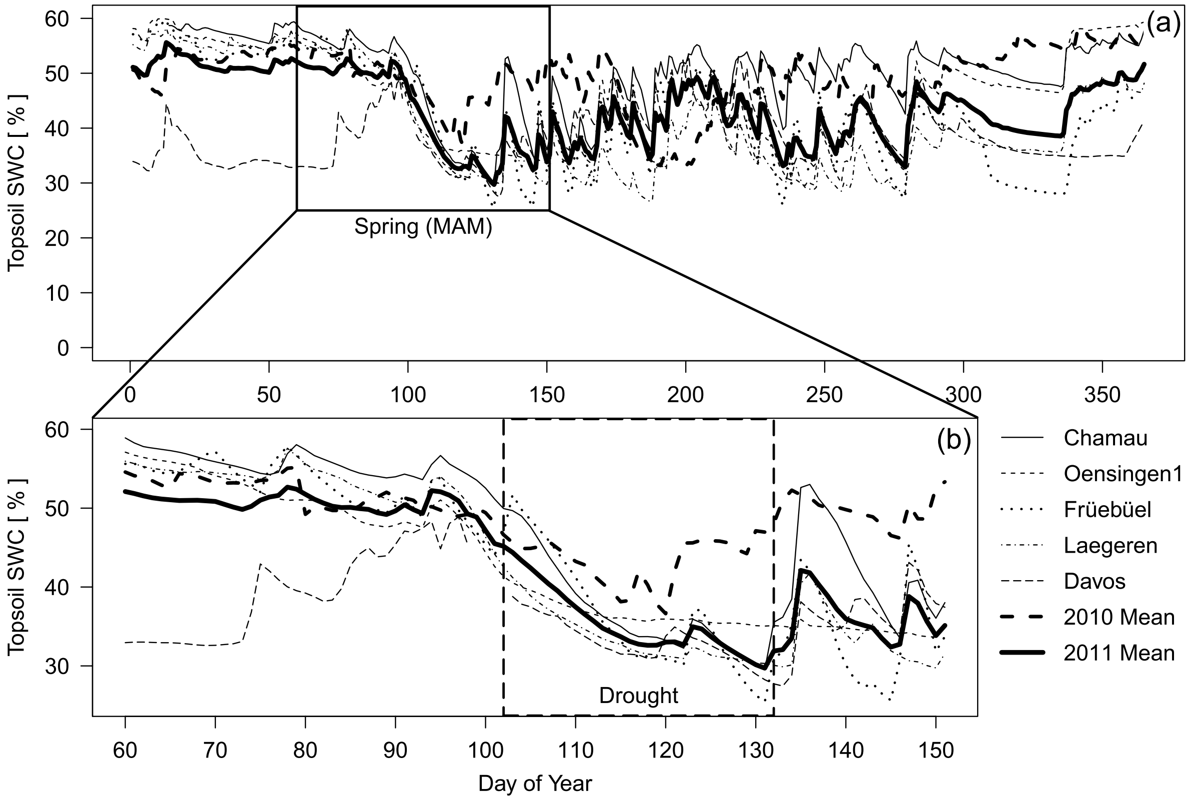

Figure 1. Daily mean volumetric soil water content (SWC) at 5 cm depth (Oensingen1: 10 cm depth) at five Swiss FluxNet sites for the full year (a) and for spring 2011 (b). For comparison, the overall mean SWC across all sites is also shown for 2010. The dashed box in (b) confines the period of spring drought across all sites (DOY 102–132).

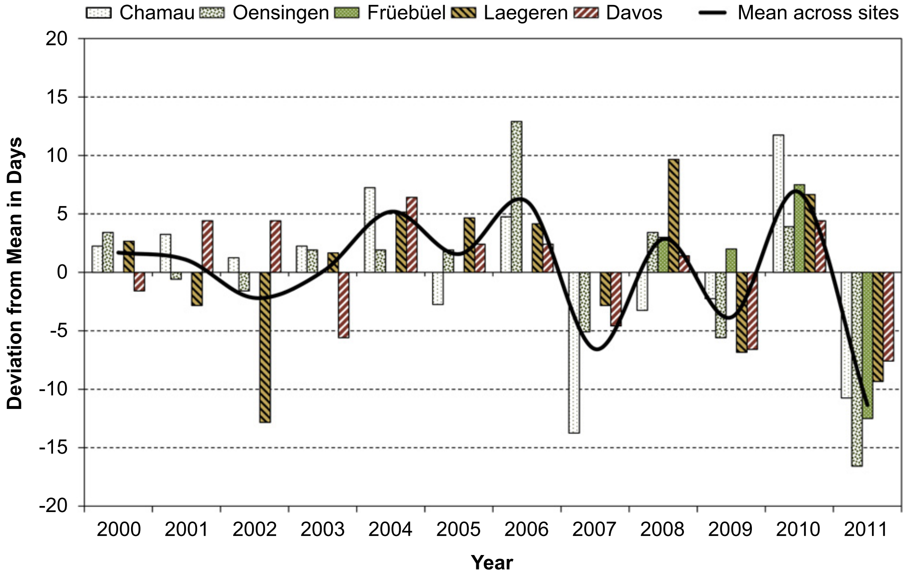

Figure 2. Site-specific phenological development compared to 2000–2011 mean of each site. Grasslands are denoted by dotted and forests by striped fill patterns. Sites are ordered according to land-use type (grassland, forest) and their respective elevational gradient from left (lowest) to right (highest). The bold black line shows the mean across all sites. Negative deviations indicate earlier, positive deviations later than average phenological development in spring. Species-specific observational data were provided by MeteoSwiss for nearby sites from the national phenological monitoring network: Davos–Norway spruce (needle emergence), Laegeren–European beech and Norway spruce (leaf unfolding/needle emergence), Früebüel, Chamau, Oensingen–Cocksfoot grass and Dandelion (full flowering). Data availability for Früebüel was limited to the years 2008–2011.

DAV: +93%) in spring 2011 (table 3). The relative change in GPP *versus* TER between these years was generally similar or larger for GPP, except at the subalpine site Davos, where higher soil temperatures in 2011 (i.e., $T_{\mathrm{Soil}} > 0\,^{\circ}\mathrm{C}$ about three weeks earlier) resulted in enhanced TER and substantially larger changes in TER compared to GPP.

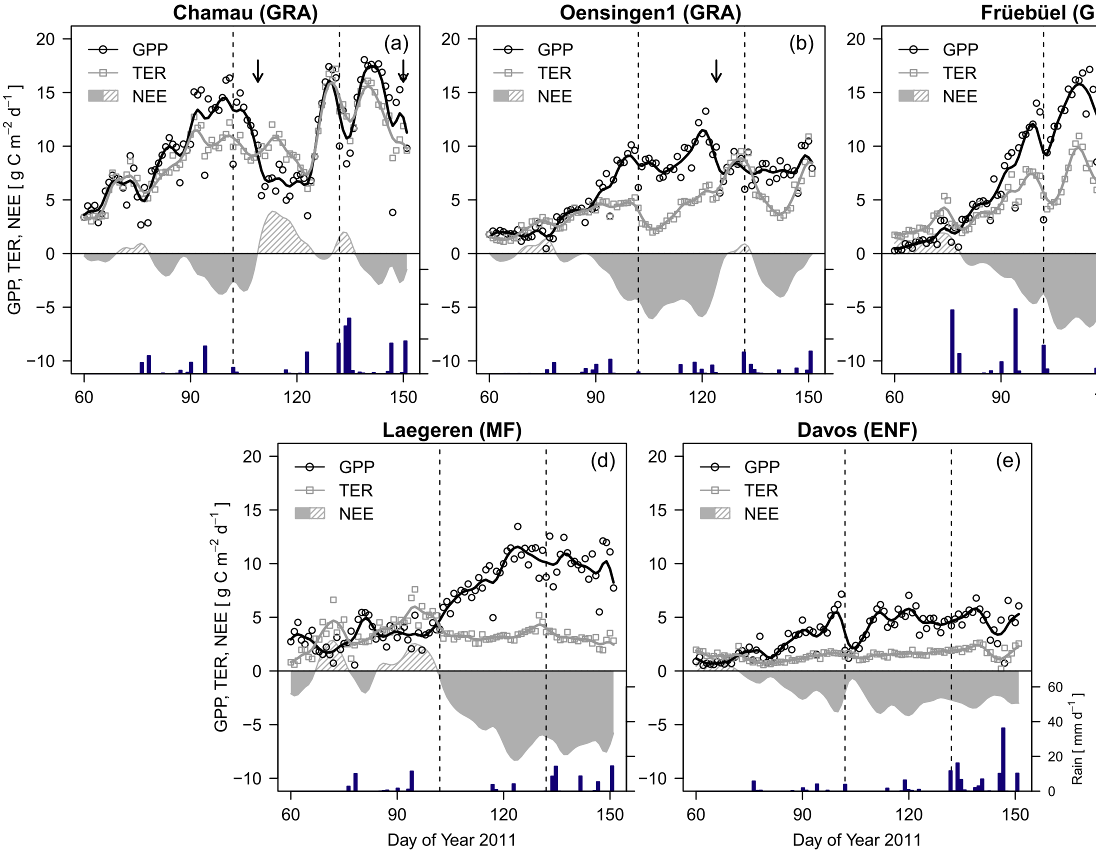

Figure 3. Daily total gross primary productivity (GPP), total ecosystem respiration (TER) and net ecosystem exchange (NEE; full shading indicates periods of carbon sink, striped shading of carbon sources) during spring 2011. Lines and shading are 7 day running means. The bars at the bottom of each panel show daily precipitation totals. Arrows indicate management at grassland sites, i.e. grass cuts (a), (b) and begin of grazing (c). The dashed lines confine the period of spring drought across all sites (DOY 102–132). Abbreviations in titles indicate the IGBP land-use class with grasslands (GRA), mixed forest (MF) and evergreen needleleaf forest (ENF). The grassland sites in the top panels are ordered according to their elevational gradient from left (lowest) to right (highest), and similarly the forest sites in the bottom panels.

Table 3. Cumulative gross primary productivity (GPP), total ecosystem respiration (TER), net ecosystem exchange (NEE), and evapotranspiration (ET) during spring (MAM) 2011. Relative deviations are reported for spring 2011 compared to 2010.

Site	Chamau	Oensingen1	Früebüel	Laegeren	Davos
GPP (g C m^{-2})	940	586	809	598	324
TER (g C m^{-2})	891	401	536	316	137
NEE (g C m^{-2})	−49	−185	−273	−282	−187
ET (mm)	181	196	233	198	125
Deviation 2011 *versus* 2010 (%)					
GPP	3	−20	38	54	19
TER	4	−20	15	23	93
NEE	−14	−21	123	114	−7
ET	−4	1	49	−21	−32

Ecosystem ET (i.e., soil and canopy evaporation plus plant transpiration) was highest at the grassland site Früebüel (2.5 ± 1.4 mm m^{-2} d^{-1}) and lowest at the evergreen forest in Davos (1.4 ± 0.8 mm m^{-2} d^{-1}, figure 4). ET was higher in 2011 than 2010 at the Früebüel grassland site (+49%) and lower at the forest sites (LAE: −21%, DAV: −32%; table 3).

3.4. Environmental controls of spring fluxes

In 2011, the main environmental controls of daily spring GPP were R_G for Chamau ($R^2 = 0.48$) and Früebüel ($R^2 = 0.67$), soil temperature for Davos ($R^2 = 0.38$), and soil moisture for Oensingen1 ($R^2 = 0.66$) and Laegeren ($R^2 = 0.76$, all $p < 0.001$, linear regression analysis). For Früebüel, soil moisture was a strong residual control of GPP ($R^2 = 0.31$, $p < 0.001$) while no significant control of moisture was detected for Chamau and Davos. Soil temperature and soil moisture were together the main environmental controls of daily spring TER for all sites, but explained a higher variability in TER for the grasslands ($R^2 = 0.54$–$0.84, p < 0.001$) compared to the forest sites ($R^2 = 0.23$–$0.47, p < 0.001$). R_G was the main environmental control for daily

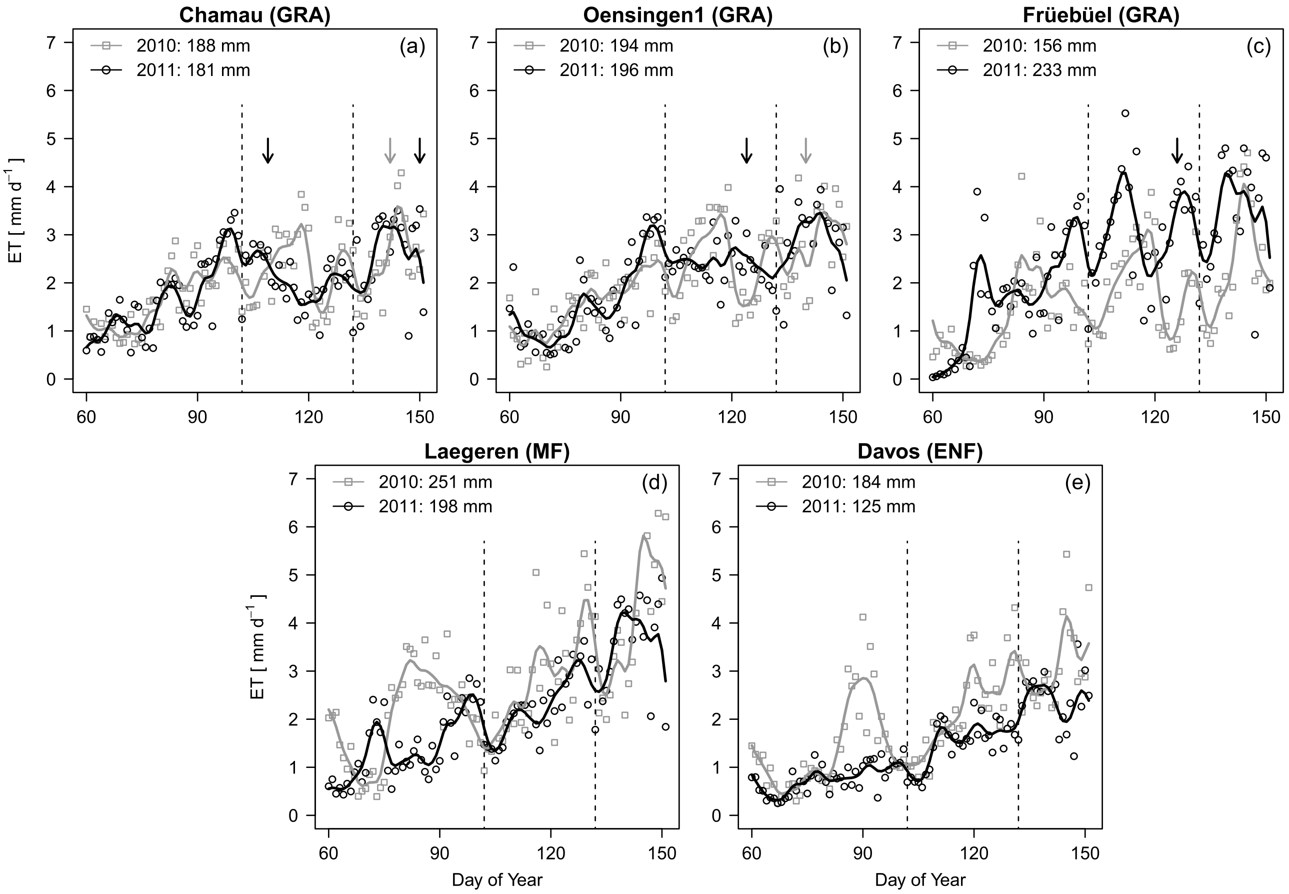

Figure 4. Daily total ecosystem evapotranspiration (ET) during spring 2010 and 2011. Lines are 7 day running means and numbers following years show total spring ET. Arrows indicate management at grassland sites, i.e. grass cuts (a), (b) and start of grazing (c). The dashed lines confine the period of spring drought across all sites (DOY 102–132). Abbreviations in titles indicate the IGBP land-use class with grasslands (GRA), mixed forest (MF) and evergreen needleleaf forest (ENF).

NEE for all grassland sites ($R^2 = 0.19$–0.67, all $p < 0.001$). In addition, spring NEE of the forest sites was driven by soil moisture at Laegeren ($R^2 = 0.66$) and air temperature at Davos ($R^2 = 0.32$, both $p < 0.001$). Low explanatory power of R_G for NEE of the grasslands Chamau ($R^2 = 0.19$) and Oensingen1 ($R^2 = 0.30$) seemed largely related to management effects (grass cuts), while grazing at Früebüel ($R^2 = 0.67$, all $p < 0.001$) had smaller effects on NEE than meteorological variables (figure 3(c)). The main driver of ET at the grassland sites was R_G, while temperature was the main control at the forest sites ($R^2 = 0.65$–0.77, all $p < 0.001$). VPD was the secondary environmental control of ET at all sites.

3.5. Carbon uptake and water deficits

We observed net carbon uptake at all sites during spring 2011, ranging from 49 g C m^{-2} for Chamau to 282 g C m^{-2} for Laegeren (figure 5, table 3). Unlike the previous year, net carbon uptake (cumulative NEE < 0) in spring 2011 generally started earlier, except for the Oensingen1 grassland. No considerable differences in NEE were found at Chamau, Oensingen1 and Davos between spring 2010 and 2011. Compared to the previous spring, substantially higher net carbon uptake was observed at the sites Früebüel (+123%) and Laegeren (+114%) in 2011.

Spring ET ranged from 125 mm at Davos to 233 mm at Früebüel (mean 187 mm; figure 4, table 3) during 2011. The difference of precipitation minus ET showed cumulative spring water deficits of −104 and −109 mm for the sites Oensingen1 and Laegeren, respectively (figure 6). Only the sites Chamau and Davos recovered from the water deficits accumulated during the drought, mainly due to substantial precipitation in the second half of May 2011. The Früebüel montane grassland had a water surplus of 120 mm at the end of spring 2011. Compared to an overall surplus of 70 mm in spring 2010, the mean water deficit was 17 mm across all sites for spring 2011.

3.6. Water-use efficiency

During spring 2011, the highest water-use efficiency (WUE, gross carbon uptake per unit water lost) was observed at the Chamau grassland (4.6 g C (kg H_2O)$^{-1}$), while the forest sites Laegeren (2.3 g C (kg H_2O)$^{-1}$) and Davos (1.9 g C (kg H_2O)$^{-1}$) showed overall much lower WUE (figure 7). Differences between spring 2011 and 2010 were insignificant at the grassland sites ($p > 0.05$), whereas WUE of the forest

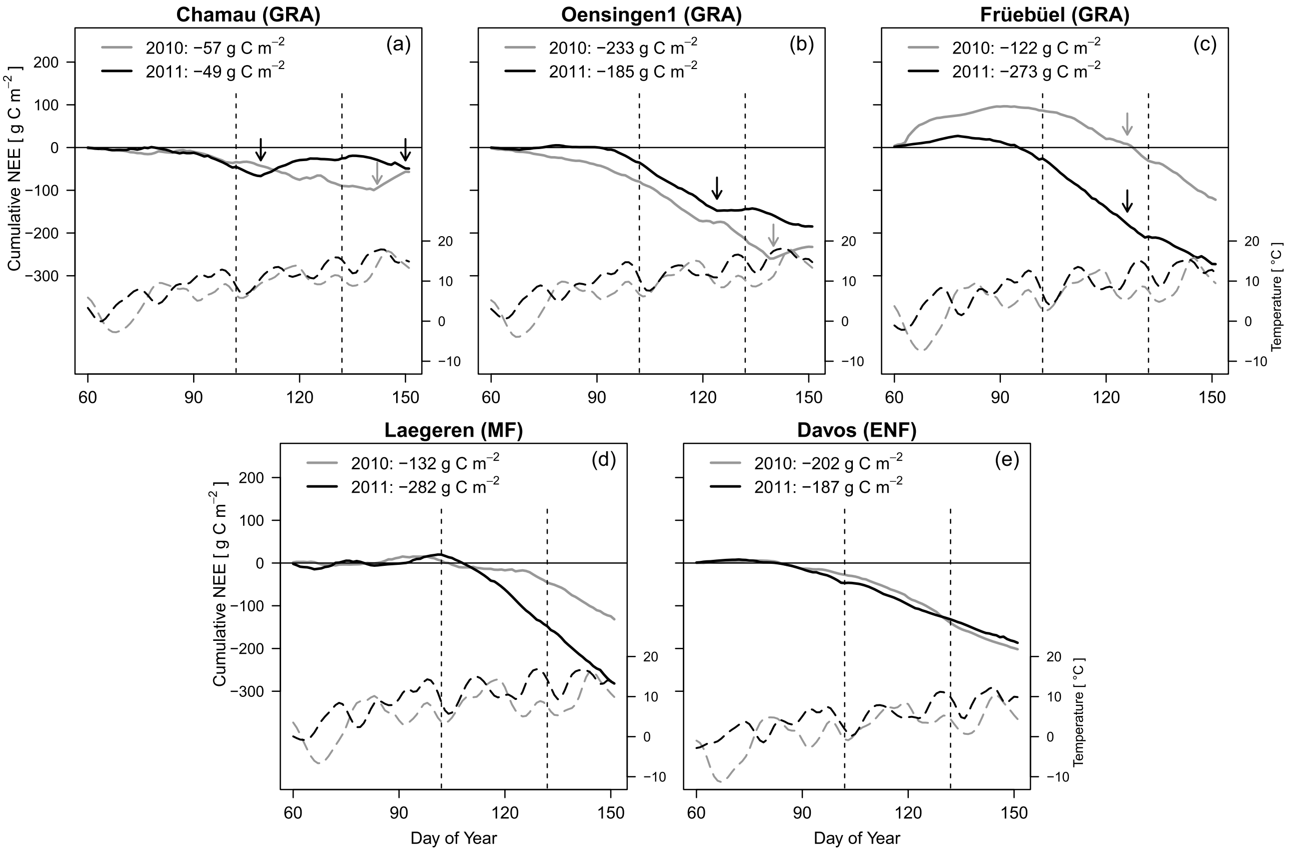

Figure 5. Cumulative net ecosystem exchange (NEE, solid lines) and air temperature (dashed lines, 7 day running mean) during spring 2010 (grey) and 2011 (black). The numbers following the years show total spring NEE. Arrows indicate management at grassland sites, i.e. grass cuts (a), (b) and start of grazing (c). The vertical dashed lines confine the period of spring drought across all sites (DOY 102–132). Abbreviations in titles indicate the IGBP land-use class with grasslands (GRA), mixed forest (MF) and evergreen needleleaf forest (ENF).

sites significantly increased (Laegeren +109%, Davos +58%, both $p < 0.001$). A combination of increased GPP along with decreased ET caused the higher WUE of the two forest sites in 2011 (table 3).

4. Discussion

Precipitation deficits during spring 2011 resulted in soil moisture deficiencies similar to those typical during summer months, persisting for an extended period (4–6 weeks) at high temperatures. While a consistently earlier phenological development was found at all sites independent of land-use type or elevation, the response of ecosystem carbon dioxide and water vapour fluxes to these spring drought conditions differed strongly among sites, in particular for water-use efficiency between forests and grasslands. Forests adapted to spring drought conditions by increasing water-use efficiency (i.e., reducing transpiration). In contrast, grasslands did not adapt and reductions in productivity of grasslands indicated soil moisture limitations inhibiting regrowth of vegetation after grass cuts during drought conditions in spring.

4.1. Phenology

The phenological development in 2011 was the second earliest since 1950 (MeteoSwiss 2011). It was largely

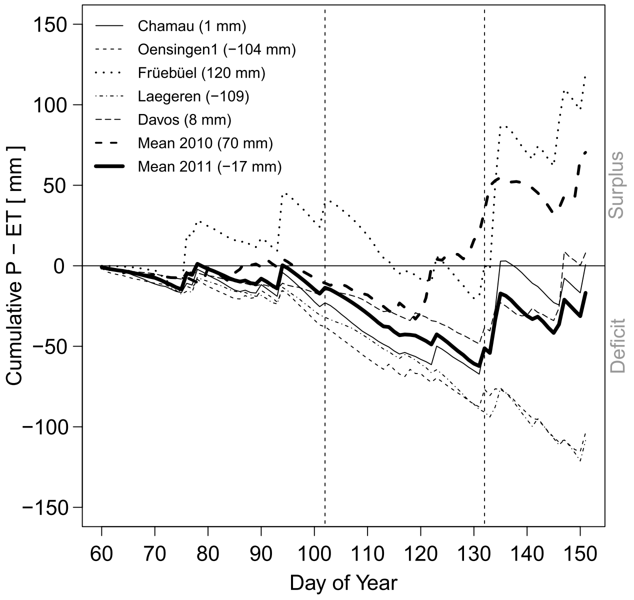

Figure 6. Cumulative daily precipitation (P) minus evapotranspiration (ET) during spring 2011. For comparison, the ensemble mean of all sites is also shown for 2010. The numbers in brackets show spring totals. The vertical dashed lines confine the period of spring drought across all sites (DOY 102–132).

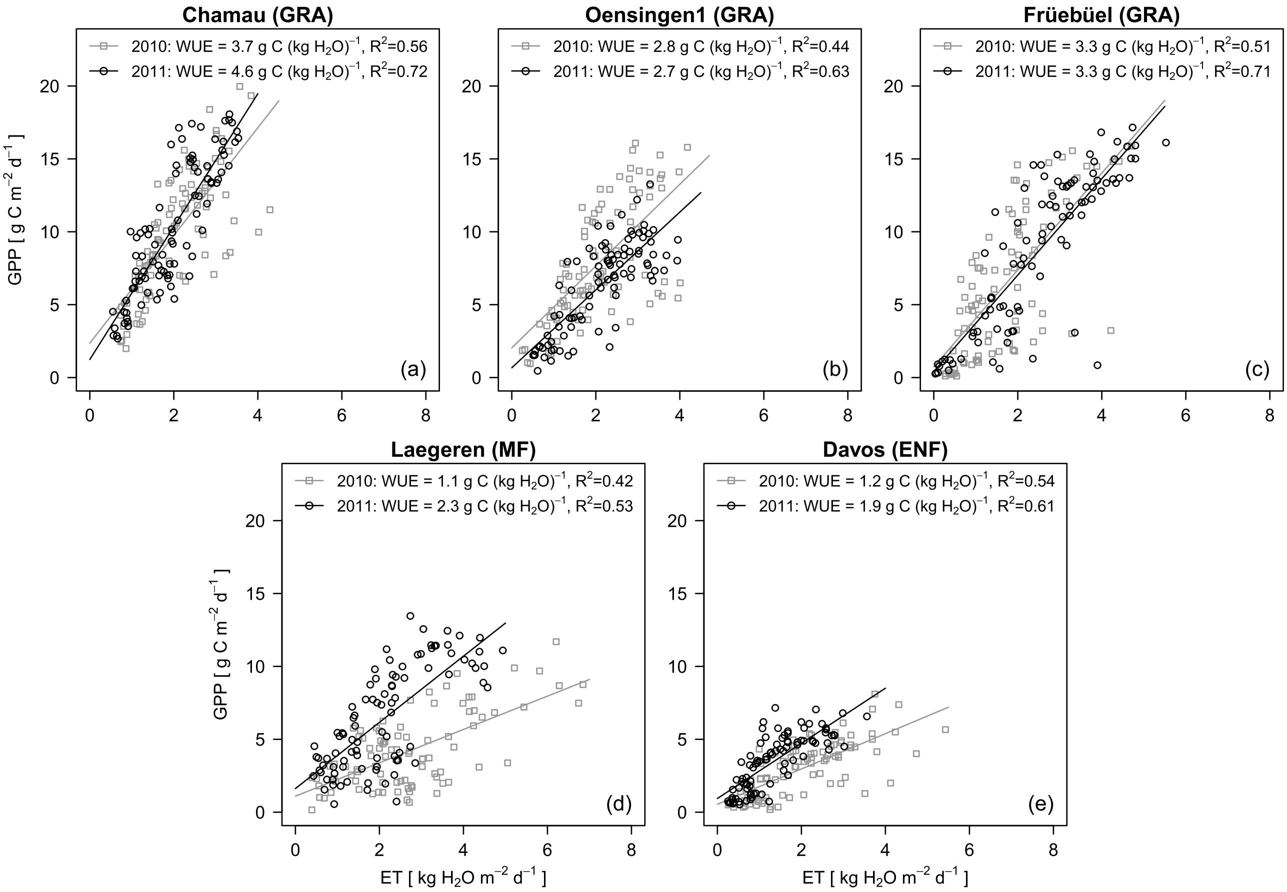

Figure 7. Water-use efficiency (WUE), i.e. the ratio of gross primary productivity (GPP) and ecosystem evapotranspiration (ET), in spring 2011 compared to 2010. Significant differences in WUE (slopes) were detected at the forest sites Laegeren (d) and Davos (e), both $p < 0.001$. Abbreviations in titles indicate the IGBP land-use class with grasslands (GRA), mixed forest (MF) and evergreen needleleaf forest (ENF).

related to temperature and none of our sites showed a delayed development related to drought. While below average precipitation was also observed during early spring 2010 (table 2), temperatures were considerably lower in 2010 (−2.7 °C), and closer to the long-term average as compared to 2011 (MeteoSwiss 2012). These differences and regression analysis (phenological development *versus* temperature) showed that temperature was the main control for spring phenology at our sites during both years ($R^2 = 0.74$, $p < 0.001$), along with photoperiod and chilling (Körner and Basler 2010), and that soil moisture limitations during spring did not inhibit the onset of leaf activity, despite strong effects on ecosystem fluxes.

4.2. Carbon uptake and gross primary productivity

In contrast to other studies that found largely reduced carbon uptake during spring drought in steppe ecosystems (Dong *et al* 2011, Parton *et al* 2012, Kwon *et al* 2008), we observed only small reductions in net carbon uptake (NEE) for some of our sites. Instead, we found substantially increased net carbon uptake of a montane grassland (Früebüel), similar to Gilgen and Buchmann (2009), and lowland mixed deciduous forest (Laegeren) in response to drought—similar to findings by Black *et al* (2000) for boreal deciduous forest in years with a warm spring. Overall, these results indicated that spring drought resulted in smaller carbon losses, which are in contrast to the substantial carbon losses that were observed during the severe summer drought in 2003 (Ciais *et al* 2005).

GPP reductions for most sites at the beginning of the drought period (DOY 102–107) were related to incoming cold air masses from the arctic (MeteoSwiss 2011) that affected in particular the higher elevation sites Früebüel and Davos, where mean temperatures dropped below 5 °C and close to freezing, respectively (figure 5). This temperature drop also reduced TER at all sites, with larger reductions observed for the grassland compared to the forest sites (figure 3).

Soil moisture related reductions in GPP were found at the lowland grassland sites, where productivity did not recover following grass cuts in Chamau mid-April (DOY 109, figure 3(a)) and Oensingen1 in early May (DOY 124, figure 3(b)). At Chamau, GPP only recovered following the next major rainfall (DOY 123). Similar reductions in grassland productivity in response to drought were found by Gilgen and Buchmann (2009) for the Chamau grassland, and by Craine *et al* (2012) for grasslands in north-eastern Kansas. In addition, the smaller net carbon uptake of Chamau seemed related to higher manure inputs compared to the Oensingen1 grassland (Zeeman *et al* 2010), which resulted in higher TER relative to GPP (ratio of 0.95 *versus* 0.68, table 3).

For both forest sites, cumulative annual net carbon uptake (not shown) started earlier in 2011 compared to 2010, 16 days at Laegeren and 13 days at Davos. These differences were similar to the results from phenological observations, which showed differences of 16 and 12 days for both forest sites between years (figure 2). The findings for Laegeren confirmed Ahrends *et al* (2009) and Etzold *et al* (2011), who reported enhanced productivity and net carbon uptake in a year (2007), when bud break at Laegeren occurred 10 days earlier compared to the two previous years (Ahrends *et al* 2009). In contrast to our two forests, we could not find a similar relation of phenological observations and NEE for the grasslands due to management at these sites, i.e., grass cuts being performed before flowering to prevent reduced biomass production after flowering.

GPP increases from 2010 to 2011 were smaller in Davos compared to Laegeren (table 3), suggesting that productivity in evergreen needleleaf forest is less sensitive to seasonal climate anomalies compared to deciduous broadleaf forest (Richardson *et al* 2010). In contrast, the opposite pattern was found for TER between both years: during spring 2011, TER was increased only marginally in Laegeren but largely enhanced in Davos (related to higher temperatures), where TER substantially exceeded the increase in GPP (table 3). This indicated limitations for higher net carbon uptake in subalpine forest ecosystems during years with above average spring temperatures—an important implication when considering the projected temperature increases for Switzerland for all seasons (CH2011 2011).

4.3. Evapotranspiration and water-use efficiency

Evapotranspiration of both forests was substantially reduced in spring 2011 compared to 2010, a clear signal of stomatal regulation (i.e., reduction of leaf transpiration) as an early response to drought (see also Jarvis and McNaughton 1986). Such regulation in forests was also shown by Teuling *et al* (2010) during a summer heatwave that was enhanced by drought: unlike grasslands, forests employ water saving strategies and reduce their ET early on, thereby reducing evaporative cooling of the atmosphere. In contrast, grasslands maintain their ET as long as soil moisture is available. In our study, grasslands did not reduce ET during spring drought either, suggesting a consistent behaviour of grassland vegetation to spring and summer droughts. The Früebüel grassland even increased ET, probably due to more available energy from clear skies during spring 2011.

In addition, both our forest sites significantly increased their WUE in response to spring drought, while no such effect was observed for the grassland sites in Switzerland. This increase in WUE is in accordance with the expected response of WUE at the leaf level, to reduce water stress while keeping foliar assimilation high (see Bacon 2004; Schulze *et al* 2005). However, such response at the leaf level does not necessarily translate to the ecosystem scale (Jarvis and McNaughton 1986), which additionally includes soil evaporation, and in fact, only few ecosystem-scale studies reported increased WUE during drought (e.g. Krishnan *et al* 2006). Nonetheless, Beer *et al* (2009) concluded from a global synthesis study of 43 flux tower sites that changes in WUE (or inherent WUE) indicate the adjustment of ecophysiology at stand level and thus enable the transfer of the WUE concept from the leaf to the ecosystem level.

The stronger increase of WUE at Laegeren (broadleaved) compared to Davos (coniferous) can be explained by stronger stomatal regulation of leaves *versus* needles (Schulze *et al* 2005), supporting results from Granier *et al* (2007) in response to the 2003 summer drought in Europe. For the same drought event, however, decreased WUE was also reported by Reichstein *et al* (2007) for mostly forest ecosystems and Hussain *et al* (2011) for a grassland. Ponce Campos *et al* (2013) recently added further evidence for higher WUE across biomes during drier years that increased with drought intensity. Therefore, further research with large observational datasets (e.g. FLUXNET) is needed to comprehensively distinguish the WUE response to drought between forests and grasslands—in general and also evaluating potential differences between spring and summer drought.

The observed water deficits (negative P-ET) or minor surplus at the end of spring could have important implications for the vegetation during summer, as spring is typically a period of water recharge for soil and groundwater reservoirs. A combination of spring and summer droughts in the same year could substantially increase the impact of summer drought, e.g. with larger reductions in productivity, enhanced temperature feedbacks amplifying heatwaves, and severe deficits in water supply for agriculture and society. In 2011, however, carry-over effects into the following season were prevented by heavy precipitation during early summer that counteracted the potential risk of extreme summer temperatures (Quesada *et al* 2012).

Overall, we conclude that forests adapt to spring drought by increasing WUE much stronger than grasslands, which could be due to an evolutionary strategy to secure carbon investments during harsh conditions (Schulze *et al* 2005).

5. Conclusions

Grasslands and forests responded very differently to spring drought in terms of ecosystem carbon dioxide and water vapour fluxes: while forests adapted and reduced their WUE significantly, grasslands did not show this behaviour, or maybe would only after a prolonged drought. These contrasting responses to drought will not only affect the feedback to the atmosphere via ET, but also indicate different susceptibilities of grasslands *versus* forests to future drought events, predicted to increase in frequency and severity. Our results further suggest that understanding the response of different land-use types to drought is highly relevant to predict impacts of climate change on biosphere–atmosphere fluxes of terrestrial ecosystems.

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Author contributions

SW conceived the study with inspiration from NB. WE, CA, MH, SZ, RH, JS and DI provided data. SW, WE and CA post-processed the data. SW performed the analyses and wrote the first draft of the manuscript. All authors contributed to data interpretation and the final manuscript.

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