

The ecological and economic consequences of shifting  
snowmelt dates and summer drought in the Alps

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## General introduction

Alpine regions above the natural climatic treeline (Körner 2012) provide multifold ecosystem services that are highly beneficial for the mountainous regions, but also for the adjacent lowlands. These ecosystem services include an exceptional biodiversity, erosion control of soils, the regulation of the water balance, and fodder production for livestock. Because of their remoteness and their scenic views, mountain regions are also highly attractive for recreational purposes and as tourist destinations. Moreover, the energy production, especially through hydropower can be of outstanding importance in these regions (e.g., Schaepli 2015; Eurac Research 2018). While 40% of the world's population depend on the provided ecosystem services, only 10% effectively live in mountainous regions (Messerli 1983; Hock et al. 2019).

In alpine regions, the anthropogenic climate change is advancing particularly fast. The warming rate of air temperature in the European Alps has been the 1.5-fold of the global average during the last decades (IPCC 2018; Hock et al. 2019). Since 1864, the yearly mean air temperature of Switzerland has already increased by 2.1 K (MeteoSchweiz 2020) and for the future, temperatures are expected to rise more rapidly at higher elevations and higher latitudes (NCCS 2018a; Hock et al. 2019). Therefore, massive implications for the snowpack have been observed, as snowmelt advanced by 5.8 days per decade between 1970 and 2015 (Klein et al. 2016). However, such results often do not refer to the alpine zone, but to regions below the upper natural treeline.

The ongoing climate change is also associated with regionally altered precipitation patterns (IPCC 2018), even though the range of uncertainty for precipitation is considerably larger (Trenberth et al. 2013; IPCC 2018). In Europe, a shift towards increased winter precipitation is expected, but going along with more frequent drought events in spring and summer (Spinoni et al. 2018). In the western Alps of Switzerland, the winter precipitation is predicted to increase by roughly 12%. But in summer, there will be ca. 20% less rain by the end of the 21<sup>st</sup> century (NCCS 2018a). For the future, it is likely that longer growing seasons will coincide with more frequent and more severe droughts (Gobiet et al. 2014). The newly developing precipitation patterns in combination with shifting snowmelt dates may have severe implications in the Alps. For instance, a retreating snow cover obviously affects winter tourism (e.g., Steiger 2010; Scott et al. 2012; Steiger and Abegg 2013; Steiger et al. 2019). Moreover, earlier snowmelt will also substantially prolong the short growing season of alpine plants. It is currently unclear whether alpine plants will profit from longer growing seasons, especially as summer drought may offset any potential benefits. Thus, the anticipated climatic changes in the Alps could have severe ecological consequences for the alpine flora, including plant phenology, plant development and nutrient cycles. Moreover, it may cause major economic burdens for winter tourism.

Already in the first IPCC report on climate change, snow cover was asserted as one of the major concerns for the future because of its obvious dependency on temperature (IPCC 1992). Because of the decreasing albedo, the warming at the snowline is even enhanced (Ceppi et al. 2012), resulting in a strong negative feedback. Because winter tourism is one of the main income sources in mountain regions, and because of avalanches as a major natural hazard, there has been a large interest in snow cover changes. For high-elevation regions (> 2000-3000 m asl), it has been controversial whether increases in the winter precipitation, and thus a higher snowpack, could compensate for the higher temperatures (e.g., Stewart 2009; Schmucki et al. 2015). In addition, Musselman et al. (2017) have recently formulated the hypothesis of «a slower melt in a warmer world». They emphasize that earlier snowmelt will evidently occur when the days are shorter and

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less solar energy is available. Thus, the melting process in the future may be slower than what we observe today.

For alpine plants above the upper natural treeline, the timing of snowmelt determines the start of the growing season. For projections of future snowmelt dates and thereby of the length of the alpine growing season, it is essential to distinguish between the effects of temperature and snow-pack height on the snowmelt date.

Switzerland has one of the highest spatial densities of snow measurement series, but most of these series stem from elevations below the climatic treeline. After the winter 1999/2000 with numerous avalanches, a new network with automatic snow depth measurements was initiated for the high alpine region above 2000 m asl (IMIS network). Many of these stations now feature time series of 20 years and may provide new insights into the high-elevation snowmelt dates and their correlations with temperature, precipitation, and snowmelt at lower elevations. This offers a unique opportunity to assess the trends (by time series analysis) in snowmelt dates for alpine regions in detail.

### *Ecological consequences of climate change*

The snow cover is a major feature of the temperate alpine region above the upper natural treeline. On 2500 m asl, the snow cover persists for roughly nine months of the year (Keller and Körner 2003, my own observations), leaving a short snow-free growing season of two to three months for alpine plants. A well-developed snow cover acts as an effective insulation against freezing temperatures (Körner 2003). The date of snowmelt determines the potential time available for growth and plant development. As an adaptation to the short growing seasons, many alpine plants have preformed buds in order to accelerate the plant development and reproduction cycle at the start of the growing season (Diggle 1997; Meloche and Diggle 2001; Körner 2003; Larl and Wagner 2006).

Under missing snow, alpine plants need a protection mechanism that inhibits them from breaking the winter dormancy too early. Keller and Körner (2003) exposed 23 alpine and nival species in growth chambers to daylengths (photoperiods) between 12 and 16 hours and for half of these species, flowering depended on the photoperiod. Similarly, Heide (1985, 1990, 2005; Heide et al. 1990) clearly demonstrated the importance of photoperiod for the development of arctic plant species. Thus, photoperiodism is a frequent adaptation to alpine and arctic environments, preventing plant development during unfavourable times of the year. In the aspect of climate change, this raises the question whether alpine plants will be capable to profit from earlier snowmelt. At the same time, field observations have revealed a high correlation of plant phenology with snowmelt dates (Canaday and Fonda 1974; Ram et al. 1988; Inouye 2008; Wipf and Rixen 2010) and with post-snowmelt temperatures (Kudernatsch et al. 2008; Hülber et al. 2010; Livensperger et al. 2016), suggesting that there may be an interaction of post-snowmelt temperatures and photoperiod. To predict future responses of alpine plant species to shifting snowmelt dates, it is crucial to explore the role of photoperiod and its interaction with post-snowmelt temperatures.

When considering post-snowmelt temperatures as well as any temperature measure for alpine plants, it is essential to account for the appropriate temperature and the plant's microclimate (Körner and Hiltbrunner 2018). The small-scale topography does not only affect snowmelt dates (e.g., Johnson and Billings 1962), but also the climate that the low-stature alpine plants experience during the growing season. Moreover, alpine plants directly affect the climate through their growth form. Owing to their small stature and dense canopies, most alpine plants operate within an aerodynamic boundary layer that thermally decouples them from free atmospheric circulation. Consequently, foliage temperatures in alpine plants are not much different from those in low

elevation grassland during bright daylight hours, which is reflected in their photosynthetic temperature response (Körner and Diemer 1987). For instance, the curled, brown leaf ends of the sedge *Carex curvula* reduce the wind speed in the canopy and create a favourable microclimate within the sedge canopy (Körner 2003, 2007). Also, flower heads of many alpine species accumulate heat (Dietrich and Körner 2014), most likely with positive effects on plant reproduction, including pollination and seed ripening. Hence, the actual climate alpine plants experience during the growing season is not well represented by air temperature measured at weather stations (Körner and Larcher 1988; Scherrer and Körner 2011; Körner and Hiltbrunner 2018).

The above-mentioned *Carex curvula* is the dominant species of late-successional, alpine grassland on siliceous bedrock, which represents one of the most abundant alpine grassland types across the European Alps (Oberdorfer 2001; Leuschner and Ellenberg 2017). Like most alpine plant species, *Carex curvula* is perennial and it mostly propagates through clonal growth by means of below-ground rhizomes (e.g., Erschbamer et al. 1994), with typical expansion rates of less than 1 mm per year (Steinger et al. 1996). Late successional grassland is highly persistent, with clone ages of *Carex curvula* of up to 4200 years (De Witte et al. 2012). Estimates for the monthly net primary production of alpine grasslands are similar as in temperate grasslands from the lowland (Körner 2003). This suggests that the short growing season limits the yearly biomass production of these ecosystems. On first glance, one might assume that the biomass production increases with earlier snowmelt and longer growing seasons. Later snowmelt in the range of one to four weeks reduced the above-ground biomass by 13% on average (compiled from 18 data sets by Wipf and Rixen 2010). Thus, time was considered as the limiting factor for growth in that study. Nevertheless it remains unclear whether the reverse - that is an earlier snowmelt - will foster the above-ground biomass production. Sørensen (1941) showed that some alpine species might have a genetically fixed length of the growing period, with cessation of growth even under favourable conditions. Thus, longer growing seasons do not necessarily stimulate above-ground biomass production.

In comparison to plants in the lowland, alpine and arctic plants generally invest more in below-ground organs (roots and storage organs; Iversen et al. 2015). They have a higher proportion of fine roots, and their specific root length is 1.5 times higher (shown for forbs; Körner and Renhardt 1987). Synchronous growth is frequently assumed for the below- and above-ground biomass (Iversen et al. 2015), but Blume-Werry et al. (2017) showed that a 8-day earlier snowmelt advanced the above-ground growth, but not that of fine roots. Also for high-latitude systems dominated by sedges, Sloan et al. (2016) observed that the growth of fine roots continued for more than a month after leaf extension had stopped. To assess whether alpine plants can profit from earlier snowmelt in terms of root growth has implications for the nutrient uptake at snowmelt and during the growing season. Thus, the below-ground biomass production should be accounted for when assessing the consequences of climatic changes on plant biomass production.

Many alpine plant species are regarded as highly resilient to drought, as revealed by the example of the alpine sedge *Carex curvula* and the forb *Primula minima*. Both showed clear signals of wilting and desiccation when they were left in a growth chamber for 44 days without watering, but fully recovered within a week after rewatering (Körner 2003). However, differences between species are large, most likely owing to their biomass allocation pattern and rooting depth. So far, the majority of drought experiments in temperate grasslands have been carried out in the lowland (e.g., Beierkuhnlein et al. 2011; Weißhuhn et al. 2011; de Vries et al. 2016), with declines in the above-ground biomass in the range of 10 to 60%. These reductions were often compensated for in the following months until winter (e.g., Hartmann and Niklaus 2012; Deléglise et al. 2015; Hofer

et al. 2016). Due to the short growing period, such a compensation may not be possible in alpine grasslands. When below-ground biomass was measured, the results between studies were inconclusive (for instance, Kahmen et al. 2005 - increase; Fiala et al. 2009 - decrease; Gilgen and Buchmann 2009 - unchanged). Thus, to increase the comparability of drought experiments worldwide, DroughtNet insists on a protocol (DroughtNet 2017). Besides a site-specific percentage of the annual precipitation that should be excluded, reports on soil texture and soil bulk density are required. Because at a given soil moisture the plant available water strongly depends on soil texture, Weng and Luo (2008) suggested that differences in the soil texture may be the major cause for inconsistent results of drought experiments.

In a truly alpine setting above the upper natural treeline, drought experiments are still rare. De Boeck et al. (2016) investigated the combined effect of heat waves and of summer drought on swards dominated by *Carex curvula* and *Nardus stricta* using monoliths with a limited rooting volume. After 17 days of rain exclusion, they observed reductions in above-ground biomass of 40 to 76% (34–49% less phytomass), along with higher amounts of necromass. Schmid (2017) experimentally induced an *in situ* summer drought (six and twelve weeks) in grassland slopes of the Swiss Alps. During two growing seasons, the author compared two regions with naturally high and low summer precipitation, respectively, and compared grasslands on siliceous and calcareous bedrock. Reductions in the above-ground biomass (12–35%) were overcompensated by an increase in below-ground production (40–80%), leading to an increase of the total biomass by 28–41%. The higher proportions of fine roots and storage organs in the top 5 cm of the soil only indicated that there was no investment into deep roots for tapping water sources deeper in the soil. In late successional alpine grasslands, around 80% of the roots are found in the uppermost 10 cm (Körner 2003).

In alpine ecosystems with nutrient-poor soils, a large proportion of the nitrogen is recycled from year to year. During plant senescence, nutrients are resorbed from the leaves (Prock and Körner 1996). For *Carex curvula*, Schäppi and Körner (1997) assessed that 68% of the nitrogen was resorbed during leaf senescence. During roots senescence 27% of the nitrogen and 57% of the phosphorus are recovered from the roots (Freschet et al. 2010). Despite this high degree of nutrient recycling, these alpine ecosystems rely on additional nutrient inputs. Additional plant available nutrients come from decomposition and mineralisation of senescing plant material (litter), from dinitrogen (N<sub>2</sub>) fixation and atmospheric nitrogen deposition (Körner 2003; Hiltbrunner et al. 2005). During drought, the decomposition and mineralisation may be slowed down by lacking water availability in the topsoil, limiting the nutrient availability in alpine grasslands (Körner 2003).

The potential consequences of shifting snowmelt dates and of summer drought have mostly been studied individually. At snowmelt, the soils are usually at field capacity (Isard 1986) and may become increasingly dry over the growing season. Thus, earlier snowmelt and longer growing seasons may amplify the effects of summer drought. To my knowledge, the only study addressing the combined effects of shifting snowmelt dates and summer drought experimentally, is a phenology study by Cornelius et al. (2013). They investigated the flowering phenology of grasslands along an elevational gradient between 600 and 2000 m asl, predominantly in the montane and subalpine vegetation zone, leaving out alpine grasslands above the upper natural treeline. Using a different approach, Iler et al. (2019) utilized long-term observations of the subalpine forb *Helianthella quinquenervis* (1999–2012). Years with early snowmelt and higher rates of flower abortion due to frost were compensated by increased flowering (more flowers) in the subsequent year. But in naturally dry years the survival rates of individual plants were reduced, letting the authors

conclude that climate change will lead to a population decline because of longer growing seasons with increased drought risk, and not due to the higher frost risk. To delineate the impact of future climatic conditions on alpine grasslands, it is thus essential that we experimentally assess the interaction of shifting snowmelt dates and summer drought on alpine ecosystems.

### *Economic consequences of climate change*

Climatic changes in alpine regions affect winter tourism, including the skiing industry.

In the mountain regions of Switzerland, every fourth person's income depends on tourism, which generates one fifth of the total income (SBS 2019). Thus, many alpine villages depend on a continuous snow cover for winter tourism. In 2007, the OECD stated that 91% of the 666 skiing resorts in the Alps were considered as naturally snow reliable. With 2 K of warming, this number would drop to 61%, or even to 30% with a warming of 4 K. As mentioned above, air temperature in Switzerland has already increased by more than 2 K during the last 150 yrs.

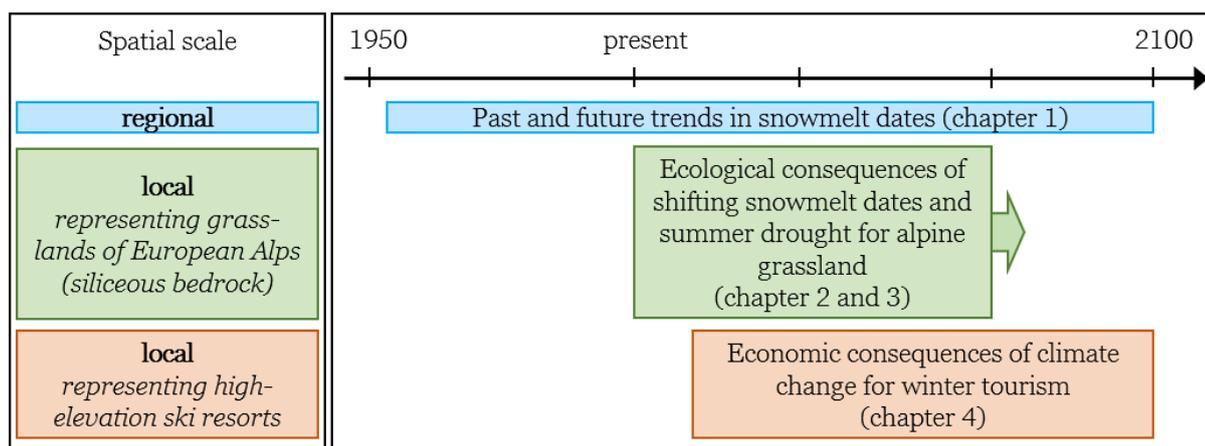
In ski resorts, snowmaking is the main adaptation to higher temperatures and less snow cover (Abegg et al. 2007; Gonseth and Vielle 2019; Steiger et al. 2019). Currently, almost half of the slopes in Switzerland are equipped for snowmaking (SBS 2019). However, to maintain a high snow reliability, ski resorts will require more snowmaking, resulting in a considerable rise of water consumption. In the future, the income of some resorts may not cover these increasing costs for water and energy (Scott et al. 2008; Steiger 2010; Rixen et al. 2011). The future shift in precipitation patterns will lead to debates and conflicts on how the water resources should be shared among various stakeholders such as skiing operators, hydropower producers, hoteliers, farmers and communities. Any investments of ski resorts in snowmaking facilities should therefore estimate (at least) the future snow reliability of the region and the resort, including the potential water consumption linked to maintaining the resort as well as other economic sectors operative.

### *Content of this PhD thesis*

This thesis was part of the transdisciplinary fellowship program «bridging plant science and society» offered by the Zürich Basel Plant Science Center (PSC) and funded by the Mercator Foundation Switzerland. Besides a strong focus on alpine plant ecology (experimental approach), the work for my thesis therefore comprised collaborations with the SLF Davos (snow cover analysis) as well as with the University of Innsbruck and the ski resort Andermatt-Sedrun-Disentis (in-depth analysis of the snow reliability of this resort by means of the model *Skisim 2.0*). I address the retracting snow cover in the Alps, its interacting effect with summer drought on alpine plants and biogeochemical cycles, as well as economic consequences for a skiing resort. Following the introduction chapter, the thesis is structured into four chapters and a concluding discussion (Figure 1).

In **chapter 1**, I start with analysing the past snowmelt dates in the Swiss central Alps (1000-2500 m asl) and projecting future trends (CH2018 scenarios), by extrapolating the effects of temperature and snowpack height. For Switzerland, increased winter precipitation is anticipated because of climatic changes. I test whether an increased snowpack height at high elevations will mitigate the effect of rising temperatures and decelerate the advancing snowmelt dates as already observed below the climatic treeline. Because snowmelt at high elevations occurs as soon as temperatures are high enough, I suspect that there is a measure for temperature that describes snowmelt dates despite large fluctuations between years and pronounced elevational shifts. Based on existing climate change scenarios, such a measure can then be applied for predicting future snowmelt dates throughout the 21<sup>st</sup> century.

Chapter 1 is published in the journal *Climatic Change*.



**Figure 1** Ecological and economic consequences of climate change in the Alps – Structure of the thesis with the considered time horizons and spatial scales

To address the consequences of shifting snowmelt dates and summer drought on the alpine vegetation, we set up a unique snow manipulation and summer drought experiment in a late successional alpine grassland at 2500 m asl. Snowmelt dates are advanced by snow removal, whereas snowmelt dates are delayed by snow addition, and summer drought is implemented by means of rainout shelters.

In **chapter 2**, I use the experimentally shifted snowmelt dates to identify the triggers of flowering phenology and I explore how summer drought interferes with those drivers. I adopt the experimental data for assessing the *in-situ* role of photoperiod. As snowmelt at 2500 m asl often occurs around summer solstice, I expect that post-snowmelt temperatures play a bigger role for the flowering phenology than photoperiod, except for years with exceptionally early snowmelt. Because the soil moisture after snowmelt is commonly high, I only expect later flowering species to be affected by summer drought.

Chapter 2 is published in the journal *Alpine Botany*.

In the framework of the snow manipulation and summer drought experiment I also examine the effect shifting snowmelt dates and summer drought on the production of above- and below-ground biomass and on litter decomposition (**chapter 3**). Earlier snowmelt may leave more time for biomass production and hence, snow removal may increase the overall biomass production. However, early snowmelt in combination with summer drought will most likely decrease the peak biomass and lead to an increased allocation of biomass below-ground. Because alpine plant species are generally drought resistant, I expect that summer drought will primarily limit the nutrient availability through reduced litter decomposition and the nutrient accessibility, manifesting through decreased nutrient uptake.

Finally, in **chapter 4**, I attend to the economic consequences of climate change for winter tourism. I conduct a case study for the ski resort *Andermatt-Sedrun-Disentis* and I explore its future snow reliability, specifically also addressing the future water consumption for snowmaking throughout the 21<sup>st</sup> century. It is likely that the natural snowpack will soon not suffice for skiing anymore. As the resort has recently invested into new snowmaking facilities, I suspect that they will mitigate the effect of increased temperatures in the short- and mid-term. However, snowmaking is not feasible at high temperatures and thus, it is thinkable that the technology reaches its limits by the end of the century, particularly at the lower elevations of the resort. The water consumption for

snowmaking will rise immensely throughout the 21<sup>st</sup> century, which will increasingly challenge the profitability of the resort.

Chapter 4 is published in the *International Journal of Biometeorology*.

## References

- Abegg B, Agrawala S, Crick F, de Montfalcon A (2007) Climate change impacts and adaptation in winter tourism. In: Agrawala S (ed) *Climate change in the European Alps - Adapting winter tourism and natural hazards management*. OECD, pp 25–60
- Beierkuhnlein C, Thiel D, Jentsch A, Willner E, Kreyling J (2011) Ecotypes of European grass species respond differently to warming and extreme drought. *J Ecol* 99:703–713. doi: 10.1111/j.1365-2745.2011.01809.x
- Blume-Werry G, Jansson R, Milbau A (2017) Root phenology unresponsive to earlier snowmelt despite advanced above-ground phenology in two subarctic plant communities. *Funct Ecol* 31:1493–1502. doi: 10.1111/1365-2435.12853
- Canaday BB, Fonda RW (1974) The influence of subalpine snowbanks on vegetation pattern, production, and phenology. *Bull Torrey Bot Club* 101:340–350
- Ceppi P, Scherrer SC, Fischer AM, Appenzeller C (2012) Revisiting Swiss temperature trends 1959–2008. *Int J Climatol* 32:203–213. doi: 10.1002/joc.2260
- Cornelius C, Leingärtner A, Hoiss B, Menzel A (2013) Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. *J Exp Bot* 64:241–251. doi: 10.1093/jxb/err313
- de Boeck HJ, Bassin S, Verlinden M, Zeiter M, Hiltbrunner E (2016) Simulated heat waves affected alpine grassland only in combination with drought. *New Phytol* 209:531–541. doi: 10.1111/nph.13601
- de Vries FT, Brown C, Stevens CJ (2016) Grassland species root response to drought: consequences for soil carbon and nitrogen availability. *Plant Soil* 409:297–312. doi: 10.1007/s11104-016-2964-4
- De Witte LC, Armbruster GFJ, Gielly L, Taberlet P, Stöcklin J (2012) AFLP markers reveal high clonal diversity and extreme longevity in four key arctic-alpine species. *Mol Ecol* 21:1081–1097. doi: 10.1111/j.1365-294X.2011.05326.x
- Deléglise C, Meisser M, Mosimann E, Spiegelberger T, Signarbieux C, Jeangros B, Buttler A (2015) Drought-induced shifts in plants traits, yields and nutritive value under realistic grazing and mowing managements in a mountain grassland. *Agric Ecosyst Environ* 213:94–104. doi: 10.1016/j.agee.2015.07.020
- Dietrich L, Körner C (2014) Thermal imaging reveals massive heat accumulation in flowers across a broad spectrum of alpine taxa. *Alp Bot* 124:27–35. doi: 10.1007/s00035-014-0123-1
- Diggle PK (1997) Extreme preformation in alpine *Polygonum viviparum*: An architectural and developmental analysis. *Am J Bot* 84:154–169. doi: 10.2307/2446077
- DroughtNet (2017) Protocol for the international drought experiment: A distributed approach to assess terrestrial ecosystem responses to extreme drought. <https://drought-net.colostate.edu/>, accessed 15 Aug 2020. p 5
- Erschbamer B, Winkler J, Wagner J (1994) The vegetative and generative development of three *Carex curvula* in the Central Alps. *Flora* 189:277–286
- Eurac Research (2018) *Ecosystem services and governance in the Alps: Tools and tips for effective environmental management and territorial development*. Bolzano, Italy. p 25
- Fiala K, Tůma I, Holub P (2009) Effect of manipulated rainfall on root production and plant belowground dry mass of different grassland ecosystems. *Ecosystems* 12:906–914. doi: 10.1007/s10021-009-9264-2
- Freschet T, Cornelissen JHC, Van Logtestijn RSP, Aerts R (2010) Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? *New Phytol* 186:879–889. doi: 10.1111/j.1469-8137.2010.03228.x

- Gilgen AK, Buchmann N (2009) Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. *Biogeosciences* 6:2525–2539. doi: 10.5194/bg-6-2525-2009
- Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J, Stoffel M (2014) 21<sup>st</sup> century climate change in the European Alps - A review. *Sci Total Environ* 493:1138–1151. doi: 10.1016/j.scitotenv.2013.07.050
- Gonseth C, Vielle M (2019) A general equilibrium assessment of climate change impacts on Swiss winter tourism with adaptation. *Environ Model Assess* 24:265–277. doi: 10.1007/s10666-018-9641-3
- Hartmann AA, Niklaus PA (2012) Effects of simulated drought and nitrogen fertilizer on plant productivity and nitrous oxide (N<sub>2</sub>O) emissions of two pastures. *Plant Soil* 361:411–426. doi: 10.1007/s11104-012-1248-x
- Heide OM (1985) Physiological aspects of climatic adaptation in plants with special reference to high-latitude environments. *Plant Prod north Proc from plant Adapt Work Tromso, Norway*, September 4–9, 1983. p 1–22
- Heide OM (1990) Dual floral induction requirements in *Phleum alpinum*. *Ann Bot* 66:687–694. doi: 10.1093/oxfordjournals.aob.a088083
- Heide OM (2005) Ecotypic variation among European arctic and alpine populations of *Oxyria digyna*. *Arctic, Antarct Alp Res* 37:233–238. doi: 10.1657/1523-0430(2005)037[0233:EVAEAA]2.0.CO;2
- Heide OM, Pedersen K, Dahl E (1990) Environmental control of flowering and morphology in the high-arctic *Cerastium regelii*, and the taxonomic status of *C. jenisejense*. *Nord J Bot* 10:141–147. doi: 10.1111/j.1756-1051.1990.tb01761.x
- Hiltbrunner E, Schwikowski M, Körner C (2005) Inorganic nitrogen storage in alpine snow pack in the Central Alps (Switzerland). *Atmos Environ* 39:2249–2259. doi: 10.1016/j.atmosenv.2004.12.037
- Hock R, Rasul G, Adler C, Cáceres B, Gruber S, Hirabayashi Y, Jachson M, Kääb A, Kang S, Kutuzov S, Milner A, Molau U, Morin S, Orlove B, Steltzer H (2019) High mountain areas. In: Pörtner H-O, Roberts DC, Masson-Delmotte V, et al. (eds) IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. In press. p 202
- Hofer D, Suter M, Haughey E, Finn JA, Hoekstra NJ (2016) Yield of temperate forage grassland species is either largely resistant or resilient to experimental summer drought. *J Appl Ecol* 53:1023–1034. doi: 10.1111/1365-2664.12694
- Hülber K, Winkler M, Grabherr G (2010) Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. *Funct Ecol* 24:245–252. doi: 10.1111/j.1365-2435.2009.01645.x
- Iler AM, Compagnoni A, Inouye DW, Williams JL, Anderson A, Miller TEX, CaraDonna PJ (2019) Reproductive losses due to climate change - induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *J Ecol* 107:1931–1943. doi: 10.1111/1365-2745.13146
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362. doi: 10.1890/06-2128.1
- IPCC (2018) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner H, et al. (eds) *Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change*. Geneva, Switzerland, pp 374–381
- IPCC (1992) *Climate change: The IPCC 1990 and 1992 Assessments*. Intergovernmental Panel on Climate Change, Canada. p 168
- Isard SA (1986) Factors influencing soil moisture and plant community distributions on Niwot Ridge, Front Range, Colorado, USA. *Arct Alp Res* 18:83–96. doi: 10.2307/1551216
- Iversen CM, Sloan VL, Sullivan PF, Euskirchen ES, McGuire AD, Norby RJ, Walker AP, Warren JM, Wullschlegel SD (2015) The unseen iceberg: plant roots in arctic tundra. *New Phytol* 205:34–58
- Johnson PL, Billings WD (1962) The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecol Monogr* 32:105–135

- Kahmen A, Perner J, Buchmann N (2005) Diversity-dependent productivity in semi-natural grasslands following climate perturbations. *Funct Ecol* 19:594–601. doi: 10.1111/j.1365
- Keller F, Körner C (2003) The role of photoperiodism in alpine plant development. *Arctic, Antarct Alp Res* 35:361–368. doi: 10.1657/1523-0430(2003)035[0361:TROPIC]2.0.CO;2
- Klein G, Vitasse Y, Rixen C, Marty C, Rebetez M (2016) Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than later snow onset. *Clim Change* 139:637–649. doi: 10.1007/s10584-016-1806-y
- Körner C (2012) Alpine treelines. *Functional ecology of the global high elevation tree limits*. Springer, Basel. p 218
- Körner C (2003) Alpine plant life. *Functional plant ecology of high mountain ecosystems*, 2<sup>nd</sup> edn. Springer, Berlin Heidelberg. p 349
- Körner C (2007) Alpine Ecosystems. *Encycl Life Sci* 1–6. doi: 10.1002/9780470015902.a0003492.pub2
- Körner C, Diemer M (1987) In situ photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Funct Ecol* 1:179–194. doi: 10.2307/2389420
- Körner C, Hiltbrunner E (2018) The 90 ways to describe plant temperature. *Perspect Plant Ecol Evol Syst* 30:16–21. doi: 10.1016/j.ppees.2017.04.004
- Körner C, Larcher W (1988) Plant life in cold climates. *Symp Soc Exp Biol* 42:25–57
- Körner C, Renhardt U (1987) Dry matter partitioning and root length/leaf area ratios in herbaceous perennial plants with diverse altitudinal distribution. *Oecologia* 74:411–418
- Kudernatsch T, Fischer A, Bernhardt-Römermann M, Abs C (2008) Short-term effects of temperature enhancement on growth and reproduction of alpine grassland species. *Basic Appl Ecol* 9:263–274. doi: 10.1016/j.baae.2007.02.005
- Larl I, Wagner J (2006) Timing of reproductive and vegetative development in *Saxifraga oppositifolia* in an alpine and a subnival climate. *Plant Biol* 8:155–166. doi: 10.1055/s-2005-872888
- Leuschner C, Ellenberg H (2017) Ecology of central European non-forest vegetation: coastal to alpine, natural to man-made habitats. *Vegetation ecology of central Europe*, Vol. II, Springer, Cham. p. 1094
- Livensperger C, Steltzer H, Darrouzet-Nardi A, Sullivan PF, Wallenstein M, Weintraub MN (2016) Earlier snowmelt and warming lead to earlier but not necessarily more plant growth. *AoB Plants* 8:plw021. doi: 10.1093/aobpla/plw021
- Meloche CG, Diggle PK (2001) Preformation, architectural complexity, and developmental flexibility in *Acomastylis rossii* (*Rosaceae*). *Am J Bot* 88:980–991. doi: 10.2307/2657079
- Messerli B (1983) Stability and instability of mountain ecosystems: Introduction to a workshop sponsored by the United Nations University. *Mt Res Dev* 3:81–94
- MeteoSchweiz (2020) Klimawandel Schweiz. <https://www.meteoschweiz.admin.ch/home/klima/klimawandel-schweiz.html>. Accessed 5 Aug 2020
- Musselman KN, Clark MP, Liu C, Ikeda K, Rasmussen R (2017) Slower snowmelt in a warmer world. *Nat Clim Chang* 7:214–219. doi: 10.1038/nclimate3225
- NCCS (2018) CH2018 – Klimaszenarien für die Schweiz. <https://www.nccs.admin.ch/nccs/de/home/materialien-und-daten/daten/ch2018-webatlas.html>. Accessed 25 Jun 2020
- Oberdorfer E (2001) Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete, 8<sup>th</sup> edition. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, 123. p 1051
- OECD (2007) Climate change in the European Alps. *Adapting winter tourism and natural hazards management*. Paris. p 136
- Prechsl UE, Burri S, Gilgen AK, Kahmen A, Buchmann N (2015) No shift to a deeper water uptake depth in response to summer drought of two lowland and sub-alpine C<sub>3</sub>-grasslands in Switzerland. *Oecologia* 177:97–111. doi: 10.1007/s00442-014-3092-6

- Prock S, Körner C (1996) A cross-continental comparison of phenology, leaf dynamics and dry matter allocation in Arctic and temperate zone herbaceous plants from contrasting altitudes. *Ecol Bull* 45:93–103
- Ram J, Singh SP, Singh JS (1988) Community level phenology of grassland above treeline in Central Himalaya, India. *Arct Alp Res* 20:325–332
- Rixen C, Teich M, Lardelli C, Gallati D, Pohl M, Pütz M, Bebi P (2011) Winter tourism and climate change in the Alps: An assessment of resource consumption, snow reliability, and future snowmaking potential. *Mt Res Dev* 31:229–236. doi: 10.1659/MRD-JOURNAL-D-10-00112.1
- SBS (2019) Saisonbilanz 2018/19. Frequentierung der Skigebiete. Seilbahnen Schweiz, Bern. p 34
- Schaeffli B (2015) Projecting hydropower production under future climates: a guide for decision-makers and modelers to interpret and design climate change impact assessments. *Wiley Interdiscip Rev Water* 2:271–289. doi: 10.1002/wat2.1083
- Schäppi B, Körner CH (1997) In situ effects of elevated CO<sub>2</sub> on the carbon and nitrogen status of alpine plants. *Funct Ecol* 11:290–299
- Scherrer D, Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *J Biogeogr* 38:406–416. doi: 10.1111/j.1365-2699.2010.02407.x
- Schmid S (2017) Impacts of climate change on alpine grassland ecosystems: Responses in structure and function. Dissertation. ETH Zürich. p 170
- Schmucki E, Marty C, Fierz C, Lehning M (2015) Simulations of 21<sup>st</sup> century snow response to climate change in Switzerland from a set of RCMs. *Int J Climatol* 35:3262–3273. doi: 10.1002/joc.4205
- Scott D, Dawson J, Jones B (2008) Climate change vulnerability of the US Northeast winter recreation-tourism sector. *Mitig Adapt Strateg Glob Chang* 13:577–596
- Scott D, Gössling S, Hall CM (2012) International tourism and climate change. *Wiley Interdiscip Rev Clim Chang* 3:213–232. doi: 10.1002/wcc.165
- Sloan VL, Fletcher BJ, Phoenix GK (2016) Contrasting synchrony in root and leaf phenology across multiple sub-arctic plant communities. *J Ecol* 104:239–248. doi: 10.1111/1365-2745.12506
- Sørensen T (1941) Temperature relations and phenology of north-east Greenland flowering plants, 9<sup>th</sup> edn. Reitzel. p 305
- Spinoni J, Vogt J V., Naumann G, Barbosa P, Dosio A (2018) Will drought events become more frequent and severe in Europe? *Int J Climatol* 38:1718–1736. doi: 10.1002/joc.5291
- Steiger R (2010) The impact of climate change on ski season length and snowmaking requirements in Tyrol, Austria. *Clim Res* 43:251–262. doi: 10.3354/cr00941
- Steiger R, Abegg B (2013) The sensitivity of Austrian ski areas to climate change. *Tour Plan Dev* 10:480–493. doi: 10.1080/21568316.2013.804431
- Steiger R, Scott D, Abegg B, Pons M, Aall C (2019) A critical review of climate change risk for ski tourism. *Curr Issues Tour* 22:1343–1379. doi: 10.1080/13683500.2017.1410110
- Steinger T, Körner C, Schmid B (1996) Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. *Oecologia* 105:94–99
- Stewart IT (2009) Changes in snowpack and snowmelt runoff for key mountain regions. *Hydrol Process* 23:78–94. doi: 10.1002/hyp
- Trenberth KE, Dai A, van der Schrier G, Jones PD, Barichivich J, Briffa KR, Sheffield J (2013) Global warming and changes in drought. *Nat Clim Chang* 4:17–22. doi: 10.1038/NCLIMATE2067
- Vorkauf M, Kahmen A, Körner C, Hiltbrunner E (2021) Flowering phenology in alpine grassland strongly responds to shifts in snowmelt but weakly to summer drought. *Alpine Botany* 131:73–88. doi: 10.1007/s00035-021-00252-z
- Vorkauf M, Marty C, Kahmen A, Hiltbrunner E (2021) Past and future snowmelt trends in the Swiss Alps: the role of temperature and snowpack. *Climatic Change* 165:44. doi: 10.1007/s10584-021-03027-x

- Weißhuhn K, Auge H, Prati D (2011) Geographic variation in the response to drought in nine grassland species. *Basic Appl Ecol* 12:21–28. doi: 10.1016/j.baae.2010.11.005
- Weng E, Luo Y (2008) Soil hydrological properties regulate grassland ecosystem responses to multifactor global change: A modeling analysis. *J Geophys Res Biogeosciences* 113:1–16. doi: 10.1029/2007JG000539
- Wipf S, Rixen C (2010) A review of snow manipulation experiments in arctic and alpine tundra ecosystems. *Polar Res* 29:95–109. doi: 10.1111/j.1751-8369.2010.00153.x





## Chapter 1 - Past and future snowmelt trends in the Swiss Alps: the role of temperature and snowpack

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### **Keywords**

Climate change, scenario modelling, time series analysis, growing season, high-elevation, IMIS

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## Abstract

The start of the growing season for alpine plants is primarily determined by the date of snowmelt. We analysed time series of snow depth at 23 manually operated and 15 automatic (IMIS) stations between 1,055 and 2,555 m asl in the Swiss central Alps. Between 1958 and 2019, snowmelt dates occurred  $2.8 \pm 1.3$  days earlier in the year per decade, with a strong shift towards earlier snowmelt dates during the late 1980s and early 1990s, but non-significant trends thereafter. Snowmelt dates at high-elevation automatic stations strongly correlated with snowmelt dates at lower-elevation manual stations. At all elevations, snowmelt dates strongly depended on spring air temperatures. More specifically, 44% of the variance in snowmelt dates was explained by the first day when a three-week running mean of daily air temperatures passed a 5 °C threshold. The mean winter snow depth accounted for 30% of the variance. We adopted the effects of air temperature and snowpack height to Swiss climate change scenarios to explore likely snowmelt trends throughout the 21st century. Under a high-emission scenario (RCP8.5), we simulated snowmelt dates to advance by 6 days per decade by the end of the century. By then, snowmelt dates could occur one month earlier than during the reference periods (1990-2019 and 2000-2019). Such early snowmelt may extend the alpine growing season by one third of its current duration, while exposing alpine plants to shorter daylengths and adding a higher risk of freezing damage.

## Introduction

The growing season of alpine plants above the climatic treeline is closely tied to snowmelt dates (e.g., Körner 2003; Hülber et al. 2010; Wipf and Rixen 2010). Therefore, the mostly long-lived alpine perennials only have about three months for their seasonal development, but there is a high local variability due to the complex topography and substantial snow redistribution by wind in winter. Most of alpine plant's growth occurs during the first few snow-free weeks (Körner 2003). In the core of the alpine vegetation belt of the Swiss Alps at 2,500 m asl, peak aboveground biomass is commonly reached in early August, thereafter photoperiod signals (daylength) trigger the resorption of nutrients from leaves (Prock and Körner 1996), followed by plant tissue senescence. The meristems of alpine plants (tissues for growth) are located a few centimeters below the ground surface and insulating snow during winter prevents soil freezing (Körner 2003). Freezing of alpine soils may alter nutrient relations by physical degradation of soil organic matter and retention of nutrients such as inorganic nitrogen (Edwards et al. 2007; Freppaz et al. 2008; Baptist et al. 2010a). Changes in the duration of the snow cover, particularly in snowmelt dates, are thus relevant for plant development and nutrient cycling in alpine ecosystems. Yet, not all alpine species may profit from earlier snowmelt, as their development may be constrained by short photoperiods (Heide 2001; Keller and Körner 2003).

### **Decline in the snow cover**

Recent climatic changes have affected the seasonal snow cover (Hock et al. 2019) and raised the concern of various stakeholders (Beniston et al. 2018), as the snowpack is crucially important for skiing and meltwater runoff affects hydropower production (Westaway 2000). In Switzerland, the number of days with snowpack has reached a minimum in the late 1980s, based on 100-year snow series from five stations between 450 and 1,860 m asl (Scherrer et al. 2013). These reductions were mainly explained by rising temperatures (Scherrer et al. 2004). By the end of the 21<sup>st</sup> century a continuous snow cover of more than 30 days will be rare in the Swiss Alps below 1,600 m asl, and the mean snow depth (Dec - Feb) is predicted to decline by 74%. Even the high-elevation station Weissfluhjoch at 2,540 m asl may undergo reductions in snow depth of 23% (Schmucki et al. 2015a). This station's snow depth has been considered to be representative for high-elevation sites (2,000-2,900 m asl) in Switzerland (Marty and Meister 2012).

Past trends in snowmelt dates, which are crucial for the alpine plant development, were assessed by Klein et al. (2016), but the analysis was restricted to 45 years and to one site in the alpine vegetation belt only. Furthermore, to predict the functioning of alpine ecosystems under climate change it is necessary to project future snowmelt dates for the alpine vegetation zone.

### **Main objectives**

We assess trends in snow onset and snowmelt between 1958 and 2019, focusing on 38 snow measurement stations between 1,055 and 2,555 m asl in the Swiss central Alps. This is a core region for winter tourism, hydropower generation, but also longer-term research projects (e.g., Körner et al. 2019). Because most time series for snowmelt dates are not longer than 20 years at high-elevation sites, we elaborate the correlation of snowmelt dates at 15 automatic stations above 2,100 m asl (daily median of 30 min intervals) with manually measured long-term series of daily snow depth data at 23 stations (mainly below 1,500 m asl). A main goal of this study was to evaluate the role of air temperatures and of the mean winter snow depth on snowmelt dates in order to predict future trends in snowmelt dates. Due to fast melting of the snowpack in spring, we

hypothesize that snowmelt dates are largely determined by the time when mean air temperatures exceed a threshold, yet to be identified. We expect that the role of mean winter snow depth regulates snowmelt dates in years with exceptionally high or low snow depth. We then apply the identified drivers of past snowmelt dates to the Swiss climate change scenarios (CH2018) to predict the onset of the alpine growing season throughout the 21<sup>st</sup> century.

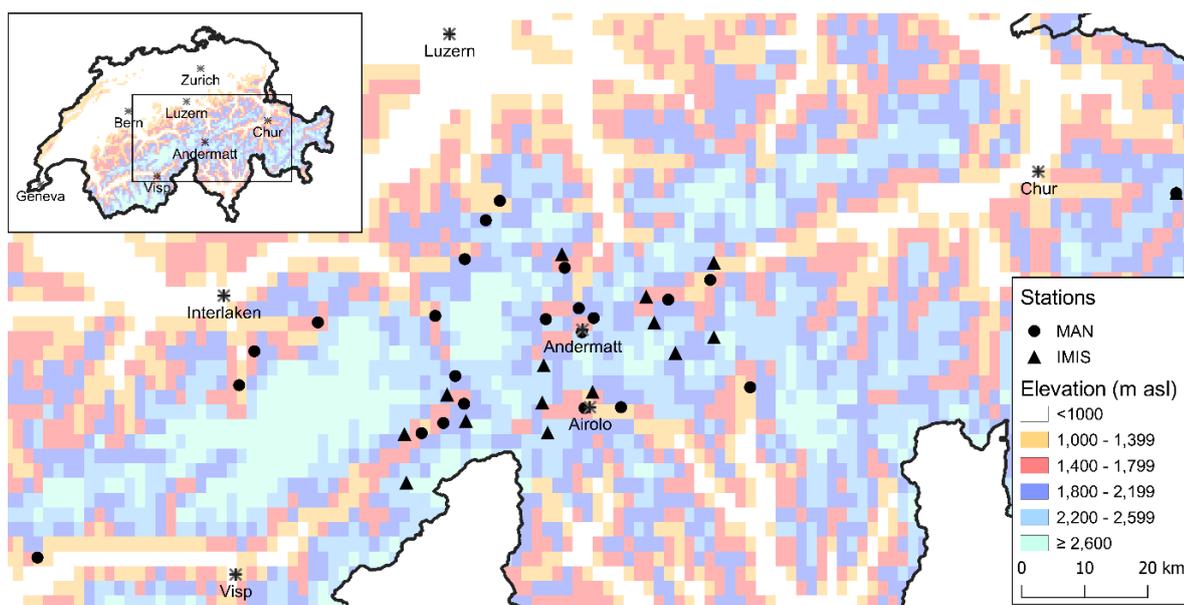
## Methods

### Station types

We analysed snow depth measurements of 38 stations between 1,055 and 2,555 m asl in the Swiss central Alps to derive time series of dates of snow onset and melt (see Table 1.1 for list of stations). We used two types of stations: manually operated (MAN) and automatic stations. MAN stations are often below 1,500 m asl, operated by the Federal Office of Meteorology and Climatology MeteoSwiss and by the WSL Institute for Snow and Avalanche Research (SLF). Snow depth readings are taken daily and many time series date back to the 1950s. Automatic stations were established to improve the Swiss avalanche warning system (Intercantonal Measurement and Information System IMIS). IMIS stations are typically located above 2,000 m asl, often close to avalanche starting zones. For most of these stations, the first fully operational year was 2000. Besides wind and temperature (air and ground), snow depth is measured by an ultrasonic sensor (SR50, Campbell Scientific, US; every 30 minutes). Both station types are typically located in relatively flat terrain. We utilized daily snow depth measurements from 23 MAN stations (morning readings) and 15 IMIS stations (daily median of 30 min snow depth values; Table 1.1). We included two stations outside of the central Swiss Alps because of their long-term data series since 1936 and 1952, respectively (Figure 1.1: 5WJ, 4MO).

### Definition of snow onset and melt

We defined snow onset and melt dates as the first and the last day of the main snow period. The main snow period corresponded to the longest period of snow cover in a hydrological year (e.g.,



**Figure 1.1** Map of manual MAN and automatic IMIS stations and the elevational belts in central Switzerland (villages and cities are presented by an asterisk; digital elevation model of the CH2018 climate change scenarios, resolution 2x2 km)

year 1991 runs from Sept 1<sup>st</sup>, 1990 to Aug 31<sup>st</sup>, 1991). Due to the two measurement techniques for snow depth and the distinct elevations, we performed different approaches to identify the main snow period of MAN and IMIS stations, respectively.

At lower elevations with MAN stations, snow-free days during winter are not uncommon and therefore, the main snow period is less clearly identifiable. For these stations, we allowed the main snow period to contain days without snow cover, but not more than 5 consecutive days. We also tested maximum gaps of 1, 3, and 10 days.

IMIS stations at high elevations with low winter temperatures show a distinct main snow period. Thus, it was unnecessary to include snow-free days for the main snow period. But the ultrasonic signal is scattered and often exhibits an offset, impeding a clear differentiation between snow cover and ground surface. Therefore, we implemented a procedure that recognizes this offset and then deduces the main snow period, including snow onset and melt dates (R function in the online resources of Vorkauf et al. 2021). To suppress the scattering, we used 5-days running means of snow depth. The snow depth signal just after snowmelt was usually less variable than for snow cover, thus, we looked for periods with relatively constant ultrasonic signals to identify the ground surface (offset). Low standard deviations (SD) of the 5-days running windows, both in winter and summer, indicated a period of constant snow depth or a period without snow (ground surface). Of all winter periods with low SD that were longer than 20 days (empirically found), we selected the most frequently occurring snow depth to obtain the height of the ground surface (offset).

At Weissfluhjoch, a MAN (5WJ) and an IMIS (WFJ2) station run in parallel (Table 1.1), which allows us to compare the snow onset and snowmelt dates deduced from the definitions for the two station types.

### Data quality and handling of data gaps

At MAN stations, the method for measuring snow depth has remained unchanged. Displacements of the measuring fields have rarely occurred and are not influential (Buchmann et al. 2020). In addition, there were no change in the sensor type of the IMIS stations nor in measuring fields through dislocations. We visually checked the snow depth data of the IMIS stations and removed obvious outliers from the data series.

For both station types, the few dates with missing snow depth data were interpolated linearly. Overall, 5% of all observations between October 1<sup>st</sup> and June 1<sup>st</sup> were missing. However, some of the MAN stations report missing values over the snow-free season. For the period between the determined snow onset and melt date, only 0.6% of the data was missing.

Missing snow onset or melt dates of single years were either filled based on correlations with nearby stations at similar elevation and comparable snow depth. If snow depth towards the end of the main snow period already went below 20 cm, snowmelt dates were extrapolated linearly (Table S1.1 lists stations and years with interpolated data gaps). In total, our data set included 1,198 observations for snowmelt dates, 2.3% of which were missing.

### Statistical analyses

Any trends in time series (onset and melt) were analysed with Theil-Sen slopes and the Mann-Kendall test (R package *trend v1.1.2*, Pohlert 2020), both relatively robust against outliers. To calculate long-term trends in snow onset and melt dates we chose the period 1958 to 2019, as it was the longest possible period with snow depth data including two stations above 2,000 m asl.

**Table 1.1** General description of all 38 stations used for identifying the snow onset and melt date, with elevation, coordinates and operational years in the Swiss central Alps. Please note that there are locations with more than one station. Stations are ordered by elevation

Type	Abbr.	Site name	Elevation	Latitude, Longitude	Canton	Operational years	Provider
MAN	GTT	Guttannen	1,055	46.6565, 8.2917	BE	1948-2019	MS
MAN	2EN	Engelberg	1060	46.8189, 8.4240	BE	1950-2019	SLF <sup>a)</sup>
MAN	GOS	Goeschenen	1,099	46.6676, 8.5811	UR	1960-2019	MS <sup>a)</sup>
MAN	AIR	Airolo	1,139	46.5260, 8.5974	TI	1959-2019	MS
MAN	1GA	Gadmen	1,190	46.7367, 8.3523	BE	1955-2019	SLF
MAN	DIS	Disentis	1,197	46.7065, 8.8534	GR	1953-2019	MS
MAN	6CB	Campo Blenio	1,215	46.5554, 8.9367	TI	1953-2019	SLF
MAN	1WE	Wengen	1,280	46.6064, 7.9213	BE	1947-2019	SLF
MAN	2ME	Meien	1,320	46.7245, 8.5568	UR	1954-2019	SLF
MAN	4UL	Ulrichen	1,350	46.5049, 8.3083	VS	1942-2019	SLF
MAN	4OW	Oberwald	1,370	46.5322, 8.3503	VS	1967-2019	SLF
MAN	4MS	Muenster	1,410	46.4904, 8.2638	VS	1946-2019	SLF
MAN	5SE	Sedrun	1,420	46.6794, 8.7688	GR	1977-2019	SLF
MAN	2AN	Andermatt	1,440	46.6332, 8.5919	UR	1941-2019	SLF
MAN	2GA	Goescheneralp	1,550	46.6518, 8.5182	GR	1989-2019	SLF
MAN	1GB	Grindelwald Bort	1,565	46.6473, 8.0514	BE	1948-2019	SLF
MAN	4MO	Montana	1,590	46.3138, 7.4770	VS	1952-2019	SLF
MAN	1MR	Muerren	1,650	46.5584, 7.8902	BE	1948-2019	SLF
MAN	6RI	Ritom Piora	1,800	46.5272, 8.6722	TI	1957-2019	SLF
MAN	GRH <sup>b)</sup>	Grimsel Hospitz	1,980	46.5715, 8.3328	BE	1950-2019	SLF
IMIS	BED3	Cassinello	2,101	46.4912, 8.5219	TI	1998-2019	SLF
MAN	GOT	Gotthard	2,107	46.5543, 8.5663	TI	1936-1970	MS
IMIS	URS2	Giltnasen	2,169	46.5871, 8.5138	UR	1998-2019	SLF
IMIS	OBW3	Maellige	2,194	46.5078, 8.3543	VS	2000-2019	SLF
IMIS	PUZ2	Ils Plauns	2,196	46.6262, 8.8626	GR	1997-2019	SLF
IMIS	TUJ3	Nual	2,211	46.6471, 8.7402	GR	1998-2019	SLF
IMIS	MEI2	Laucheren	2,220	46.7435, 8.5509	UR	1998-2019	SLF
IMIS	TUJ2	Culmatsch	2,262	46.6843, 8.7236	GR	1998-2019	SLF
IMIS	VAL2	Vallascia	2,268	46.5492, 8.6135	TI	1997-2019	SLF
MAN	GUE <sup>c)</sup>	Guetsch	2,287 2,283	46.6535, 8.6162 46.6524, 8.6150	UR	1958-2003 2009-2019	MS
IMIS	LUM2	Lumpegna	2,388	46.7317, 8.8621	GR	1998-2019	SLF
IMIS	GOM3	Treichbode	2,427	46.4891, 8.2286	VS	2000-2019	SLF
IMIS	OBW2	Jostsee	2,432	46.5454, 8.3161	VS	2000-2019	SLF
IMIS	GOM2	Bodmerchumma	2,439	46.4212, 8.2328	VS	2000-2019	SLF
IMIS	BED2	Cavanna	2,450	46.5340, 8.5108	TI	1997-2019	SLF
MAN	5WJ	Weissfluhjoch	2,540	46.8296, 9.8092	GR	1937-2019	SLF
IMIS	WFJ2	Weissfluhjoch	2,536	46.8296, 9.8093	GR	2000-2019	SLF
IMIS	LUK2	Lai Verd	2,555	46.6040, 8.7830	GR	2000-2019	SLF

<sup>a)</sup> SLF: Institute for Snow and Avalanche Research; MS: Federal Office of Meteorology and Climatology MeteoSwiss

<sup>b)</sup> HS measurements for the entire main snow period started in 1970

<sup>c)</sup> The data of two stations were combined to obtain a complete dataset for the location (referred to as one station). At the station GUE the manual measurements were replaced by automatic measurements in 2009

This period included 16 MAN stations between 1,055 and 2,555 m asl with continuous measurements for snow depth.

As snowmelt dates are more decisive for alpine plant development than snow onset, we focussed on snowmelt dates for the further analysis. However, both, snow onset and snowmelt dates were needed to delineate main snow cover duration. Short-term trends in snowmelt dates were computed as Theil-Sen slopes by running windows of 21 years for all 23 MAN stations, each covering at least the period 1958-2019 except for GOT at 2,107 m asl (1936-1970). The trend in year  $y$  corresponded to the trend for the years  $y-10$  to  $y+10$ . IMIS stations could not be included in the analysis of running window trends, as they did not cover the required 21 years. Thus, we compared high (IMIS stations) and low-elevation (MAN stations) sites by the Pearson correlation between their snowmelt dates. For each station we computed the yearly deviation of snowmelt dates from its mean between 2000-2019. Thereof, we calculated the yearly mean and SD of the deviation for each station type. A prerequisite for the correlation of time series is the so-called weak stationarity, where the expected mean, variance, and covariance do not change over time. A commonly adopted approach is to subtract from each value the value from the previous year (Cryer and Chan 2008). For the so derived first-differences of the snowmelt series, we then calculated the Pearson correlation between snowmelt dates at MAN and IMIS stations.

To project future snowmelt dates, we unravelled the contributions of temperature and snow depth to snowmelt dates by fitting a model including both parameters and their relationships with snowmelt dates. For snow depth, we used the mean snowpack height  $HS_{\text{mean}}$  between snow onset and snowmelt date, available from the daily snow depth measurements. Automatic weather stations (MeteoSwiss) measure the daily mean air temperature 2 m above ground. For nine of the MAN stations, air temperature measurements from the same location (village), usually within less than 100 m elevational difference were available: GOS (27; means 27 years of overlapping snow depth and temperature data at a given site), GTT (37), 4UL (39), GRH (50), GUE (58), DIS (59), 5WJ (60), 4MO (68), and 2AN (79). The temperature data have already undergone a semi-automatic quality control, and we used homogeneous data series for GTT, 4UL, GRH, GUE, DIS, 5WJ, 2AN. The 14 IMIS stations recorded air temperatures every 30 minutes during 20 years (WFJ2 was excluded due to the parallel station 5WJ, see Table 1.1 for abbreviations).

Snowmelt dates differ between stations (elevations) and fluctuate over the years. Thus, the time when temperatures are high enough for snowmelt to occur also varies between stations and years. As we observed that the snow depth rapidly decreases during the last weeks before the snowmelt date, we assumed that the snowmelt date would only occur when air temperatures were high enough for a certain time period. We thus adopted a temperature measure for the first day (day of year DOY) when the daily mean air temperature exceeded 5 °C in a running window of 21 days ( $T_{21d} \geq 5 \text{ °C}$ ). We empirically found a high correlation of  $T_{21d} \geq 5 \text{ °C}$  with the snowmelt dates ( $r = 0.87$ ,  $p < 0.001$ ). As snowmelt occurs at temperatures above 0 °C we also tested a threshold of 0 °C and 3 °C, and for an upper limit we used a threshold of 10 °C. Moreover, we tested running windows of 7, 14 and 30 days, and also degree-days with thresholds  $>0 \text{ °C}$  and  $> 5 \text{ °C}$ , all yielding weaker correlations (shown in Figure S1.1). Moreover, our prior exploration of the data implied a high linear correlation of the snowmelt dates with the square root of  $HS_{\text{mean}}$  ( $r = 0.85$ ,  $p < 0.001$ ).

We thus fitted the linear mixed model:

$$SM_{station} = a * T_{21d} \geq 5 \text{ } ^\circ\text{C} + b * \sqrt{HS_{mean}} + intercept_{station} \quad (\text{Eq. 1}),$$

where  $a$  indicates how much the snowmelt date was delayed by an additional day of  $T_{21d} \geq 5 \text{ } ^\circ\text{C}$  (unit day day<sup>-1</sup>);  $b$  (day cm<sup>-1/2</sup>) describes the non-linear relation of snowmelt dates and the square root of  $HS_{mean}$ , and  $intercept_{station}$  is the intercept of stations used as random factor. We visually checked residuals of the linear mixed model and excluded 33 data points (outliers) with large residuals and high leverage from the analysis. Because  $T_{21d} \geq 5 \text{ } ^\circ\text{C}$  and  $HS_{mean}$  may be correlated, we also calculated the variance inflation factor. This factor indicates how much variance of a variable is influenced (inflated) due to collinearity with another variable. To assess their individual effect on snowmelt dates, we also fitted linear mixed models for either of the two fixed effects,  $HS_{mean}$  or  $T_{21d} \geq 5 \text{ } ^\circ\text{C}$ . For each model, we derived the marginal  $R^2_m$  that showed the percentage of variance explained by the individual fixed effect, along with the conditional  $R^2_c$  that explained the variance by the fixed and random effects combined (R package *MuMIn v1.43.15*; Bartoń 2020).  $R^2_m$  allowed us to quantify the contributions of both,  $HS_{mean}$  and  $T_{21d} \geq 5 \text{ } ^\circ\text{C}$  to snowmelt dates.

### SM in the 21<sup>st</sup> century

To estimate trends in snowmelt dates for the 21<sup>st</sup> century, we applied the above linear mixed model to the CH2018 Climate Change Scenarios for Switzerland (CH2018 Project Team 2018). These include three Representative Concentration Pathway scenarios, referred to as: RCP2.6 (strong emission reductions, warming limited to 2 °C, 12 simulations), RCP4.5 (declining emissions after 2050, > 2 °C warming compared to pre-industrial times, 25 simulations), and RCP8.5 (unabated emissions, 31 simulations). For these simulations, a total of 31 regional climate models of the EURO-CORDEX (Jacob et al. 2014) were used, all exhibiting resolutions of 12 or 50 km. Downscaled scenarios (quantile mapping method) are available for seven of the MAN stations considered here (2AN, 4MO, 4UL, 5WJ, DIS, GRH, GUE), and also as a 2x2 km grid over Switzerland (CH2018 2018). For the further analysis, we used the scenarios for these seven MAN stations (between 1,197 and 2,540 m asl) and for the IMIS stations, we extracted the simulation parameters from this 2x2 km grid. All simulations provided projections for air temperature, thus  $T_{21d} \geq 5 \text{ } ^\circ\text{C}$  was estimated accordingly. To account for elevational differences between IMIS locations and grid cells, we applied an air temperature lapse rate of -0.5 K per 100 m increase in altitude (results for lapse rates between -0.2 and -0.8 K per 100 m are provided in Figure S1.3). As the scenarios include projections for precipitation, we deduced  $HS_{mean}$  from accumulated winter precipitation. For the seven MAN stations, we first determined the sum of the measured daily precipitation starting at October 1<sup>st</sup> until  $T_{21d} \geq 5 \text{ } ^\circ\text{C}$  (DOY). We only considered days with daily mean temperatures  $\leq 0 \text{ } ^\circ\text{C}$  during the period between 1982 and 2019. We calculated Pearson correlations of the so derived cumulative precipitation and of the  $HS_{mean}$  for the seven stations. We then computed a station-specific proportionality factor of the cumulative precipitation in relation to the  $HS_{mean}$  (mean accumulated precipitation per cm of snowpack height). For IMIS stations, which commonly do not measure precipitation, we used the mean proportionality factor of the seven MAN stations (1,197-2,540 m asl).

### Model validation

To assess the model's performance, particularly, with measured  $HS_{mean}$  *versus* parameterised  $HS_{mean}$  (Eq. 1), we refitted the linear mixed model with empirical data of the seven MAN stations from uneven years only. We subsequently used the measured and the parametrised  $HS_{mean}$  to

predict snowmelt dates of uneven years and compared the model results to the observed snowmelt dates. In a second step, we applied the original model to the reference periods of the climate change scenarios, 1990 to 2019 (MAN), and 2000 to 2019 (IMIS), respectively. For these 30 and 20 years, we compared estimated and observed snowmelt dates as well as trends (Theil-Sen slopes) of the snowmelt date time series (estimated vs. observed).

We then projected future changes in snowmelt dates for the three 30-year periods 2020-2049 (beginning of century), 2045-2074 (mid-century), and 2070-2099 (end of century) as well as for the 21<sup>st</sup> century (2020-2099) to achieve future longer-term trends of snowmelt dates, determining the onset of the alpine growing season. All calculations and analyses were performed with R 3.6 (R Core Team 2019).

## Results

### Comparison of definitions for snow onset and snow melt

We carefully assessed the suitability of our definitions for snow onset and melt dates. The main snow period at MAN stations was only slightly affected by the maximum number of consecutive snow-free days we allowed for. In 53% of all cases, snowmelt dates were the same, irrespective of the number of snow-free days. The 5-day-gap we used for the further analysis yielded the same snowmelt dates as gaps of 3 days in 86% of all cases.

Snow onset at both station types at the Weissfluhjoch (Table 1.1) differed by no more than one day in 11 out of 19 overlapping years. However, late autumn snowfall in two years was classified as part of the main snow period at the MAN station, resulting in a difference of 10 and 17 days compared to the IMIS station. Snowmelt was slightly earlier at the MAN than at the IMIS station, with a median difference of one day, and a maximum difference of four days in 2000 and 2010. This variation in snowmelt dates was most likely caused by micro-topographical differences (slight topographical depression).

**Table 1.2** Trends (Theil-Sen slopes) for the snow onset and snowmelt dates between 1958 and 2019 with the corresponding p-value (Mann-Kendall test). Positive values indicate a trend towards later in the year, negative values towards earlier in the year. Bold p-values indicate statistically significant trends. Stations are ordered from low to high elevation (lowest first)

Station abbr	Site name	Snow onset		Snowmelt	
		Trend 1958-2019 (days decade <sup>-1</sup> )	p-value	Trend 1958-2019 (days decade <sup>-1</sup> )	p-value
GTT	Guttannen	+0.6	0.74	- 3.0	0.08
2EN	Engelberg	+0.6	0.68	- 3.5	0.06
1GA	Gadmen	+0.5	0.64	- 1.2	0.26
DIS	Disentis	+1.7	0.24	- 1.4	0.28
6CB	Campo Blenio	+2.2	0.14	- 1.5	0.14
1WE	Wengen	+1.4	0.39	- 2.9	0.03
2ME	Meien	+2.6	<b>0.03</b>	- 6.3	<b>&lt; 0.01</b>
4UL	Ulrichen	+1.4	0.22	- 2.0	<b>0.04</b>
4MS	Muenster	+2.4	0.09	- 2.7	<b>0.02</b>
2AN	Andermatt	+1.5	0.19	- 3.6	<b>&lt; 0.01</b>
1GB	Grindelwald Bort	+1.5	0.31	- 2.9	<b>0.02</b>
4MO	Montana	+0.5	0.78	- 3.1	<b>0.01</b>
1MR	Muerren	+1.2	0.34	- 0.8	<b>0.42</b>
6RI	Ritom Piora	+3.0	<b>0.02</b>	- 2.8	<b>0.01</b>
GUE	Guetsch <sup>a)</sup>	-	-	- 3.1	<b>0.01</b>
5WJ	Weissfluhjoch	+0.4	0.76	- 4.0	<b>&lt; 0.01</b>

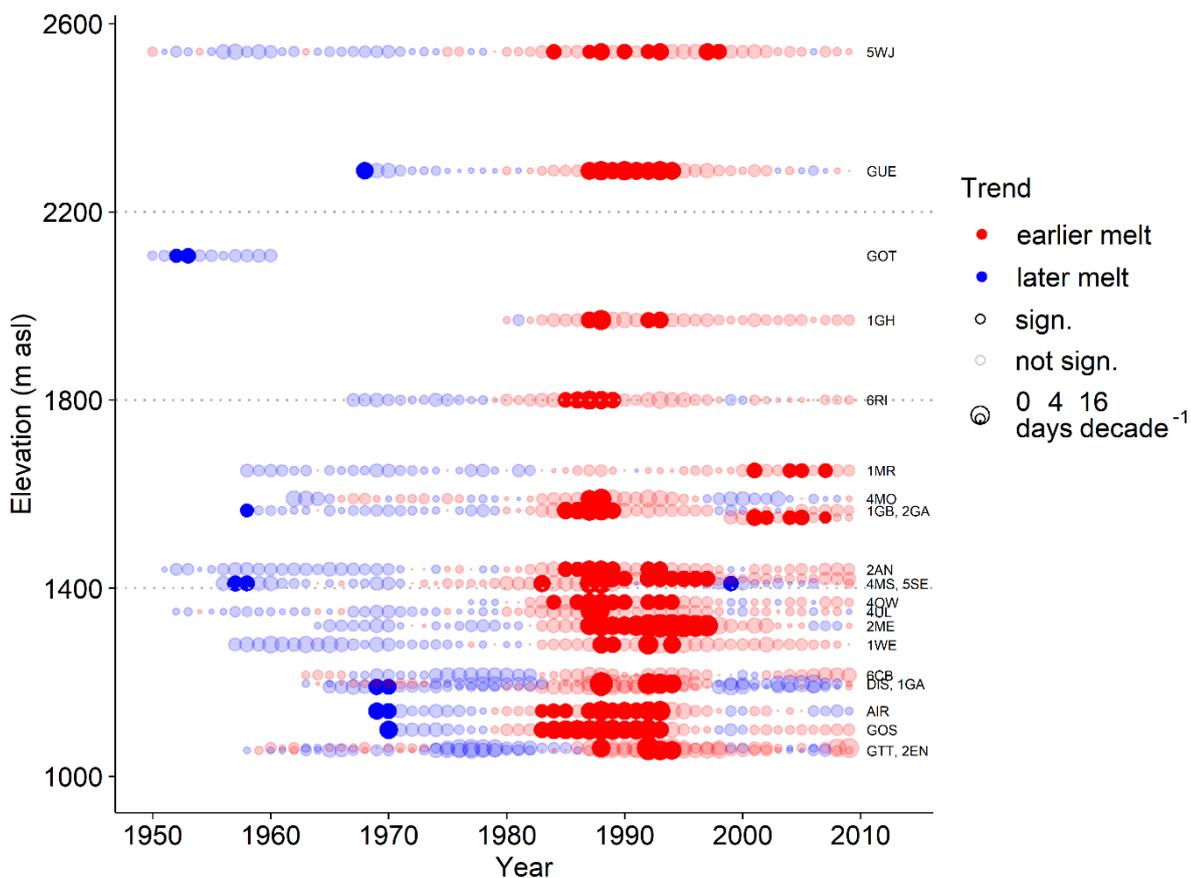
<sup>a)</sup> No continuous records for OS

### Trends in snow onset and melt dates: 1958 to 2019

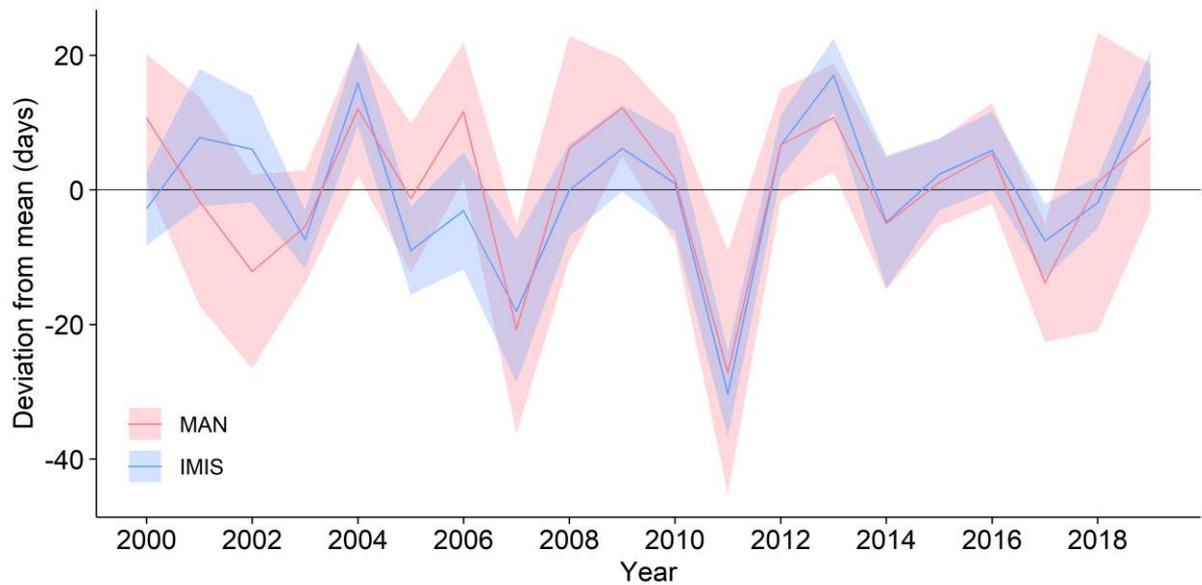
Out of the 38 stations, 16 MAN stations had continuous snow depth recordings for the past 62 years or more. To assess relevant shifts across time and elevations, we calculated the trends in snow onset and melt dates for the period 1958 to 2019. There was a tendency towards later snow onset that was indicated by persistently positive Theil-Sen slopes. These trends were statistically significant for two stations only: 2ME, 6RI (Table 1.2). In contrast, there was a clear trend towards earlier snowmelt and for ten stations, this shift was statistically significant ( $p < 0.05$ ). Across all stations, snowmelt on average occurred  $2.8 \pm 1.3$  days (mean  $\pm$  sd) earlier per decade. The magnitude of the trends in snowmelt did not depend on elevation ( $p = 0.46$ ;  $R^2 = 0.04$ ) and at the two stations in the alpine vegetation zone (GUE, 5WJ), snowmelt occurred 3.1 and 4.0 days earlier per decade (Table 1.2). With 6.3 days per decade, the station 2ME (1,320 m asl) showed the most distinct shift in snowmelt dates.

### Trends in snowmelt dates: 21-years running window trends

Trends of 21-year running windows revealed the temporal variability of snowmelt date trends between 1946-2009. We required continuous snowmelt date time series of at least 21 years, excluding the IMIS stations. Our analysis unveiled a period with later snowmelt dates during the 1940s to 1980s, but trends were rarely statistically significant. Strikingly, the late 1980s and early 1990s were denoted by a sharp, significant trend towards earlier snowmelt, with a mean of  $15.1 \pm 3.8$



**Figure 1.2** Snowmelt trends in 21-year running windows at MAN stations, ordered by elevation. The colours indicate the direction of the trend. The symbol size corresponds to the slope of the trend (expressed in days per decade) and opaque fillings represent statistically significant trends at  $p < 0.05$  (see Table 1 for station abbreviation and full station name, respectively). For instance, a trend for the year 2009 (last dot) corresponds to the Theil-Sen slope for the period 1999 to 2019



**Figure 1.3** Yearly deviation of snowmelt dates from the 10-year average (2000-2009) for manual MAN (red,  $n = 22$ ) and automatic IMIS stations (blue,  $n = 15$ ; mean [line]  $\pm$  sd [bands]). The deviation at single stations is shown in Figure S1.4

days per decade in 1988 (1978 – 1998,  $n_{\text{stations}} = 21$ ; Figure 1.2). This pattern was evident for nearly all stations and along all elevations, even at the highest location (5WJ, 2,540 m asl). Only two stations (1MR, 6CB) did not show this shift. After the 1990s, trends in snowmelt dates did not exhibit a consistent direction and they were mainly statistically non-significant. The clear trend towards earlier snowmelt for the whole period between 1958 and 2019 was caused by the abrupt shift during the late 1980s and early 1990s.

### Comparison of snowmelt dates at MAN and IMIS stations

As high-elevation stations were scarce in the past, we compared snowmelt dates of IMIS and MAN station during 2000 and 2019, with measurements for both station types. Between 2000 and 2019, average snowmelt at the IMIS stations (2,101-2,555 m asl) was in mid-June around the longest day of the year, whereas at the MAN stations (1,055-1980 m asl without GUE and 5WJ) snowmelt occurred in mid-April. The Pearson correlation for the yearly mean snowmelt dates of the two station types was 0.83 ( $n_{\text{years}} = 20$ ,  $p < 0.01$ ; Figure 1.3). Even without the two MAN stations above 2,000 m asl (5WJ and GUE), this correlation was strong (0.82,  $n_{\text{years}} = 20$ ,  $p < 0.01$ ). This means the changes in snowmelt dates at stations above the climatic treeline (IMIS stations) are closely related to these at lower-elevation MAN stations. There was one exception in 2002 with the second warmest February since the start of measurements at that time, followed by a warm spring, causing early snowmelt at low elevation (12 days earlier than the mean at MAN stations). Whereas at high elevation, large precipitation amounts in February, March and May 2002 fell as snow, thus delayed snowmelt (six days later than the mean at IMIS stations).

### Influence of $HS_{\text{mean}}$ and temperature on snowmelt dates

Air temperature and  $HS_{\text{mean}}$ , as a proxy for accumulated winter precipitation, directly influenced snowmelt dates along the whole elevational range of the stations. We quantified both effects by analysing snowmelt dates in relation to the observed  $T_{21d} \geq 5$  °C and  $HS_{\text{mean}}$  (Figure 1.4; stations at 1,055-2,540m asl; variance inflation factor of 1.04). For each week that this 5 °C threshold was

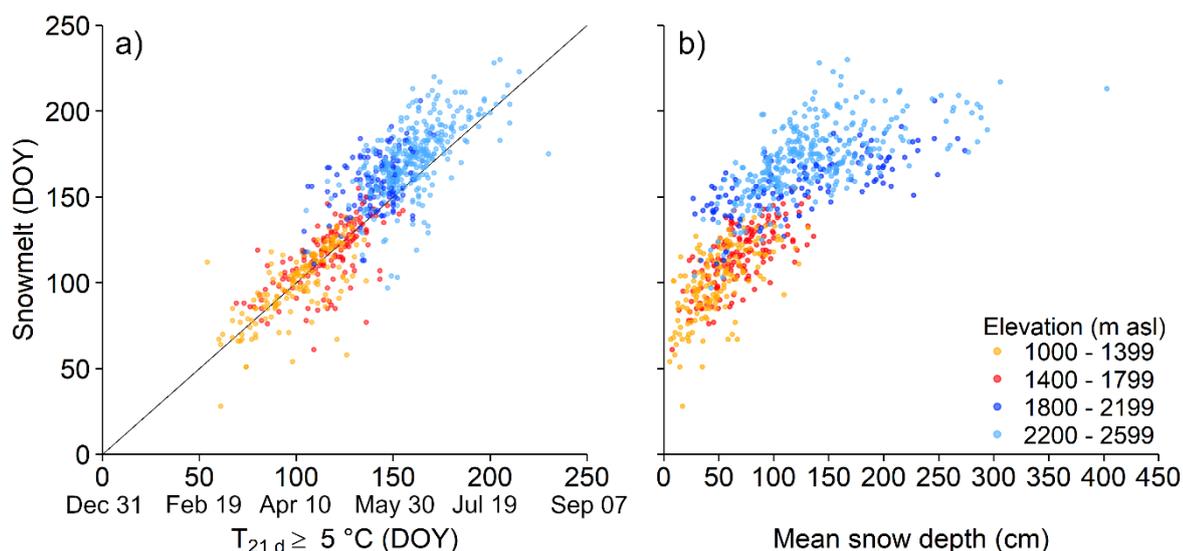
attained earlier, mean snowmelt dates occurred 3.9 days earlier ( $a = 0.6$  days  $\text{day}^{-1}$  in Eq. 1). The model with  $T_{21d} \geq 5$  °C explained 44% of the variance in snowmelt dates ( $R_c^2$  0.81). A higher  $HS_{\text{mean}}$  delayed snowmelt, proportionally to the square root of  $HS_{\text{mean}}$  (Figure 1.4b;  $b = 4.6$  days  $\text{cm}^{-1/2}$  in Eq. 1). For instance, an increase of  $HS_{\text{mean}}$  from 40 to 90 cm caused a delay in snowmelt dates by 14 days, but an increase from 140 to 190 cm postponed snowmelt by nine days only. In the model with  $HS_{\text{mean}}$  only, still 30% of the variance in snowmelt dates was explained ( $R_c^2$  0.80). Together,  $T_{21d} \geq 5$  °C and  $HS_{\text{mean}}$  explained 80% of the variance in the snowmelt date ( $R_c^2 = 0.89$ ).

### Snowmelt throughout the 21<sup>st</sup> century

We projected future snowmelt dates by applying the linear mixed model to the CH2018 Climate Change Scenarios (CH2018 Project Team 2018). For the seven MAN stations with scenarios for temperature and precipitation, a  $HS_{\text{mean}}$  of 100 cm on average corresponded to an accumulated winter precipitation of  $560 \pm 70$  mm (minimum of 460 mm in 4MO, maximum of 650 mm at GRH) and disclosing no effect of elevation. The correlation of  $HS_{\text{mean}}$  and the total winter precipitation for the period 1982 to 2019 was high, with Pearson correlation coefficients between 0.74 (DIS) and 0.86 (4UL). Only at the station Guetsch (GUE) it was lower, with 0.65.

Compared to the observed snowmelt dates, the predicted snowmelt dates for even years (model refitted with data of uneven years only) had a standard error of less than one day (0.82 days), highlighting a good model fit. With  $HS_{\text{mean}}$  estimated by the station-specific proportionality factors, the standard error increased by 15% to 0.94 days.

For our model validation, we used the reference period of the climate change scenarios: 1990 to 2019 (MAN) and 2000 to 2019 (IMIS). At MAN stations, medians of the observed and simulated snowmelt dates deviated by zero to seven days only. The median snowmelt date of IMIS stations was also well reproduced by the model outputs. Deviations of one (TUJ2) to 14 days (OBW2)



**Figure 1.4** Snowmelt a) in relation to the first day (day of the year; date) when the running mean air temperature of a 21-days window reaches a threshold of 5 °C ( $T_{21d} \geq 5$  °C), and b) in relation to the mean snow depth between snow onset and melt date ( $HS_{\text{mean}}$ ). The 755 data points are from 10 MAN (1941-2019) and 14 IMIS stations (2000-2019), but not every station covers the entire time span)

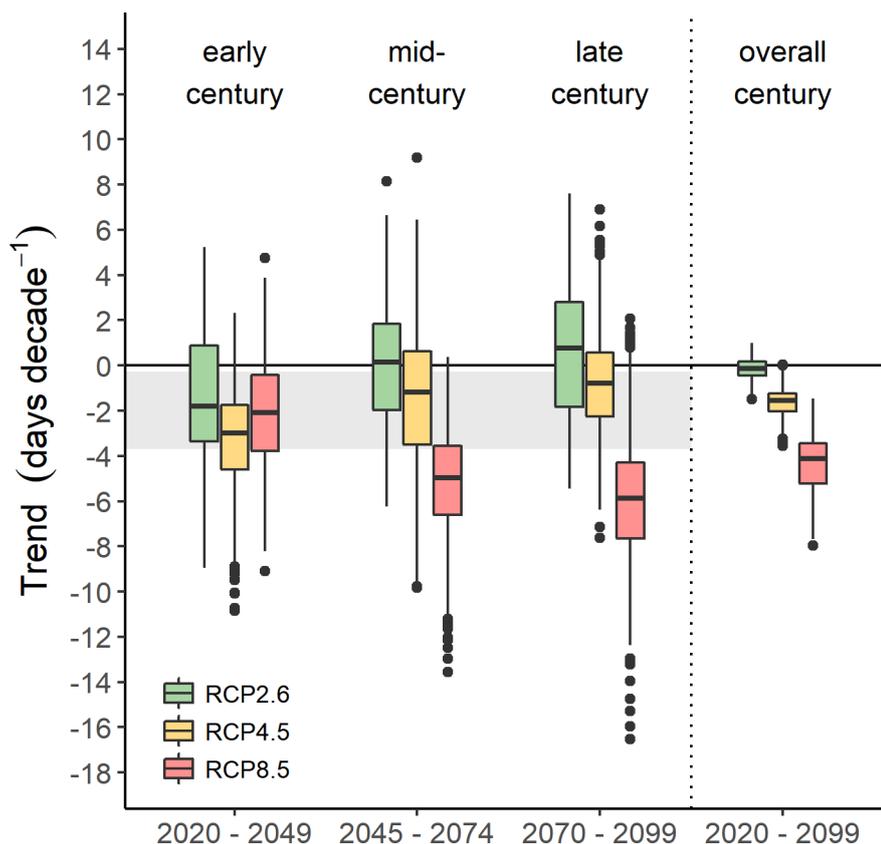
were overall larger than at MAN stations, because the model parameters extracted from a 2x2 km grid did not always mirror the exact station conditions (estimated vs. observed snowmelt in Figure S1.5). The time series analysis of the observed snowmelt dates revealed no significant trend during the reference period, except for one station (10 days decade<sup>-1</sup> at TUJ3,  $p = 0.03$ ). Most CH2018 simulations for the reference period did not display significant trends in the snowmelt date either. However, on average 11% of the simulations at MAN station featured significant trends towards earlier snowmelt, and 7% at IMIS stations, but without uniform direction. After the validation, we simulated the future snowmelt dates based on CH2018 projections for the beginning of the 21<sup>st</sup> century (2020-2049), for the mid-century (2045-2074), and for the end of the century (2070-2099) as well as the overall trend for the 21<sup>st</sup> century (2020-2099; Figure 1.5). The trends of the simulated time series of snowmelt dates within each RCP were relatively concise regarding their direction. A 1,000 m elevational gradient caused a decrease in median snowmelt trends by 0.5 days decade<sup>-1</sup> only, thus the magnitude of the effect of elevation was negligible ( $p = 0.17$ ,  $R^2 = 0.10$ ). We here present the rates of change (trends) in snowmelt dates throughout the 21<sup>st</sup> century as the median trend across stations (7 MAN and 14 IMIS stations) and of a total of 68 simulations (12 for RCP2.6, 25 for RCP4.5, and 31 for RCP8.5). Extreme trends in snowmelt (outliers in Figure 1.5) were clearly identifiable as results of single simulations and not because we aggregated stations of different elevations. As there were no large differences in trends between MAN and IMIS stations, we combined the results (Figure 1.5) and we rounded our estimations to whole numbers (Table 1.3).

In RCP2.6, predicted snowmelt dates did not show any change throughout the 21<sup>st</sup> century. Under RCP4.5, median snowmelt dates throughout the century will occur 2 days earlier each decade and 81% of the trends were statistically significant. This overall trend was mainly caused by a pronounced advancement during the beginning of the century (2020-2049, Figure 1.5), with 3 days per decade. This shift dropped to 1 day per decade by the end of the century. For the whole century, the RCP4.5-models projected the median snowmelt date to advance by 10 days by the mid-century, and by 13 days by the end of the century (Table 1.3).

With unabated emissions (RCP8.5), snow will melt 4 days earlier each decade between 2020 and 2099 (trends of all simulations at all stations statistically significant). In contrast to the other two RCP scenarios, we found that snowmelt dates will accelerate over the century. While at the beginning, snowmelt will occur 2 days earlier per decade, towards the end of the century it will be 6

**Table 1.3** Projected deviation of snowmelt dates compared to the reference period (MAN: 1990-2019, IMIS: 2000-2019; median, 25<sup>th</sup> and 75<sup>th</sup> quantiles, expressed as number of days: negative values mean earlier snowmelt, positive later snowmelt) for the future 30-year periods and three RCP scenarios. All values are rounded to whole days

Period	Scenario	Median (days)	0.25 quantile (days)	0.75 quantile (days)
2020 - 2049	RCP2.6	-5	-14	4
	RCP4.5	-5	-13	3
	RCP8.5	-6	-14	2
2045 - 2074	RCP2.6	-6	-15	3
	RCP4.5	-10	-19	-2
	RCP8.5	-14	-25	-5
2070 - 2099	RCP2.6	-5	-14	3
	RCP4.5	-13	-22	-4
	RCP8.5	-27	-39	-16



**Figure 1.5** Projected trends in snowmelt dates of 21 (7 MAN and 14 IMIS) stations throughout the 21<sup>st</sup> century for the three emission scenarios RCP2.6, RCP4.5 and RCP8.5. In total 68 simulations based on downscaled regional climate models: 12 for RCP2.6, 25 for RCP4.5, and 31 for RCP8.5, whereby the uneven sample sizes are responsible for the variability of trends between RCP scenarios in the early century. The coloured box contains 50% of all simulations per RCP scenario and time period. The region shaded in grey indicates the 25<sup>th</sup> and 75<sup>th</sup> quantile trend during the 30-year period 1990 to 2019

days earlier per decade. Median snowmelt dates will be 14 days earlier in the mid-century and 27 days earlier by the end of the century (Table 1.3).

To further illustrate the effect of these trends, we took a closer look at 2AN at 1,440 m asl, a touristic skiing resort in central Switzerland, and at the two highest IMIS stations BED2 (2,450 m asl) and LUK2 (2,555 m asl). During the reference period (1990-2019), the median snowmelt date in 2AN occurred in late April, and only once before April 1<sup>st</sup> (2011). Under RCP4.5, snowmelt before April could become normal in one out of 12 winters, and under RCP8.5, this would be the case in one out of four years. At the IMIS stations BED2 and LUK2, earliest snowmelt was at the beginning of June during 2000 to 2019, and the median snowmelt date was in the first third of July. In one out of four winters, snowmelt will occur in the first half of June (RCP4.5) or even before June 1<sup>st</sup> (RCP8.5).

## Discussion

### Past trends of snowmelt dates

Between 1958 and 2019, snowmelt occurred  $2.8 \pm 1.3$  days earlier per decade. This was substantially more conservative than the 5.8 days per decade stated by Klein et al. (2016) for the period 1970 to 2015. We could associate these different rates to the specific time periods. Trends in snowmelt dates varied considerably throughout the past decades, as revealed by trends in 21-

years running windows. The late 1980s and early 1990s were marked by substantially earlier snowmelt dates. This so-called regime shift manifested itself by earlier snowmelt and caused a 20% reduction of snow days above 1,300 m asl in Switzerland (Marty 2008a). Moreover, rapid climatic shifts during the late 1980s were evident in other datasets around the globe, e.g. ocean and air temperatures, sea ice extent, and grape ripening dates (Reid et al. 2016). In Switzerland, March to May temperatures increased by  $0.39 \text{ K decade}^{-1}$  between 1959 and 2008 (Ceppi et al. 2012), and by  $0.84 \text{ K decade}^{-1}$  in the period 1975 to 2004 (Rebetez and Reinhard 2008), suggesting that spring temperatures caused the regime shift in snowmelt dates described above. For Europe, this regime shift has recently been explained by natural, coincidental anomalies in the atmospheric circulation that were possibly related to the Pacific Decadal Oscillation and the Arctic Oscillation. This short-term warming superimposed a long-term trend of rising temperatures (Sippel et al. 2020). Locally, as for example in Switzerland, the decline of these atmospheric anomalies even led to a (short-term) trend towards lower temperatures (Ceppi et al. 2012; Bader and Fukutome 2015; Saffioti et al. 2016). Indeed, MeteoSwiss highlighted the dominant role of cyclonic low-pressure weather situations over Europe during winters (Dec-Feb) since the 1990s. Accordingly, we do not see any clear trends in snowmelt dates after the regime shift. Colder winters due to large-scale weather phenomena over Europe may thus have masked the recent warming and slowed the retreating snowmelt dates.

### **The role of elevation**

Most studies on snow cover changes (e.g., Laternser and Schneebeli 2003; Scherrer et al. 2004; Marty 2008; Klein et al. 2016) focussed on stations at lower elevation, including only a few in the alpine vegetation belt (e.g., Gr. St. Bernard, Weissfluhjoch). Here, we included the relatively new snow depth series of IMIS stations and clearly demonstrated that the snowmelt dates correlated well with MAN stations, despite the two-months earlier snowmelt dates at lower elevations. We did also not find a pronounced elevational gradient in the trends of snowmelt dates. Scherrer et al. (2004) observed an only weak elevational gradient for the snow days (Dec-Feb) along an elevational gradient between 400 and 2,500 m asl. Laternser and Schneebeli (2003) highlighted that the snow cover duration shortened fastest between 1,000 and 1,600 m asl, because temperature increases close to the zero-degree isotherm had the largest impact on the snow cover (Ceppi et al. 2012). The advancement of snowmelt dates at lower elevations may be slowed down by the reduced amount of solar radiation that is available when snowmelt dates recede towards earlier in the year (Musselman et al. 2017). At higher elevations, where the snowpack may persist beyond the mid-summer, receding snowmelt dates may move to a time with highest solar radiation and thermal energy and trends may therefore be accelerated (Essery et al. 2020).

Counter to our expectations, our proportionality factor describing the relation of winter precipitation to  $HS_{\text{mean}}$  was unaffected by elevation. We would have assumed a temperature dependence, due to a higher fraction of liquid precipitation at lower elevations. However, under-catch and wind-induced snow redistribution at high elevations may potentially balance out the effect of an elevational gradient.

The RCP scenarios displayed slightly more moderate trends at higher elevations. But with less than  $0.5 \text{ days decade}^{-1}$  for 1,000 m elevational difference, this was negligible.

### **Effect of temperature and precipitation on snowmelt dates**

Temperature and precipitation, the two key factors for determining snowmelt dates, are highly affected by climate change (IPCC 2013). Morán-Tejeda et al. (2013) emphasized temperature as

the driving factor for the snowpack duration below 1,200 m asl. Above this elevation, accumulated precipitation and the winter-history of temperature and precipitation were more influential. For snowmelt, we found  $T_{21d} \geq 5 \text{ }^\circ\text{C}$  to be 1.5 times more influential than the precipitation proxy  $HS_{\text{mean}}$ . Moreover, snowmelt dates related to the square-root of  $HS_{\text{mean}}$ , revealing a decreasing influence of snow depth at higher elevations. Our measures for temperature and precipitation thus differed from monthly mean air temperatures and accumulated precipitation considered in Morán-Tejeda et al. (2013).  $T_{21d} \geq 5 \text{ }^\circ\text{C}$  represents a threshold when temperatures are high enough for the whole snowpack to melt. Although  $HS_{\text{mean}}$  correlates with accumulated winter precipitation, it does not always directly relate to monthly precipitation. Both our measures account for the temperature and precipitation history during winter.

### Snowmelt dates throughout the 21<sup>st</sup> century

Accelerating snowmelt dates above the climatic treeline can only be halted by abating emissions enormously, as our simulations predict a roughly one-month earlier snowmelt for RCP8.5 and two-week earlier snowmelt for RCP4.5 by the end of the 21<sup>st</sup> century. Compared to previous projections of snow cover changes, our estimations are rather conservative. Bavay et al. (2009) projected snowmelt dates in Eastern Switzerland to occur 40 days earlier by the end of the century, and in the large Aare catchment (3,190 km<sup>2</sup>) the snow duration at 2,000 m asl may shorten by 2.5 months compared to the reference period (1999-2012; Marty et al. 2017). Such early melt could be interpreted as a direct consequence of lower snow depth and snow water equivalents, as simulated by Schmucki et al. (2015) and Steger et al. (2013). In contrast to these studies, our model is fully based on empirical observations and not on physical processes. Our data used for model fitting covered a period with massive changes in snowmelt dates, nevertheless, the relation of  $T_{21d} \geq 5 \text{ }^\circ\text{C}$  and  $HS_{\text{mean}}$  to the snowmelt date was robust.

### Consequences for alpine plants

Our simulation results also allow us to put alpine snow manipulation experiments into the context of climate change scenarios. Some experiments realised 18 days earlier snowmelt dates by reducing the snow depth in spring, summarised by Wipf and Rixen (2010). Under RCP8.5, these experiments would thus reproduce conditions we may observe in the mid-century (2045-2074). A one-month earlier snowmelt may expand the alpine growing season by more than one third by the end of the century (RCP8.5), most likely with drastic consequences for alpine plants. These may include lower flower numbers, reduced leaf growth and a lower survival, as observed for the evergreen forb *Gentiana nipponica* by a one-month earlier snowmelt (Kawai and Kudo 2018). And snowbed species produced less seeds after an earlier snowmelt of 18 days (Tonin et al. 2019). According to an experiment with 23 nival and alpine species, it is assumed that one third to one half the alpine flora may be sensitive to photoperiod and hence, may not profit from longer growing season because of too short daylengths (Keller and Körner 2003). The 4h-difference in daylength they applied in the greenhouse study is comparable to snowmelt in mid-March instead of late June, a shift of roughly three months. Such a shift exposes plants to higher frost risks. Recurrent frosts killed flower buds in alpine herbs (Inouye 2008), impaired growth snowbed species (Baptist et al. 2010b) as well as in three dwarf shrub species (Wipf et al. 2009). Francon et al. (2020) further suggested a strong elevational impact, disclosed by growth ring analysis of the shrub *Rhododendron ferrugineum*. Longer growing seasons at 2,400 m asl enhanced its growth, while at 1,800 and 2,000 m asl early snowmelt dates led to frosts and ultimately limited growth.

Because a one-month earlier snowmelt will not reduce the daylength sufficiently for photoperiod restrictions, we assume that in the long-term, frost events at the beginning of the growing season will play a bigger role than photoperiod limitations and may diminish the effect of longer growing seasons.

## Conclusions

We show a high correlation between snowmelt dates at high-elevation IMIS stations and lower-elevation MAN stations, implying that snowmelt dates are advancing with similar rates along an elevational gradient of 1,000 m asl to 2,500 m asl in the Swiss Alps. Our empirical approach highlighted the dominant effect of temperature over a slightly weaker influence of mean snow depth ( $HS_{\text{mean}}$ ) on snowmelt dates. With  $T_{21d} \geq 5 \text{ }^\circ\text{C}$  we found an appropriate temperature measure that correlated well with snowmelt dates at different elevations. By applying both,  $T_{21d} \geq 5 \text{ }^\circ\text{C}$  and  $HS_{\text{mean}}$  to CH2018 Climate Change Scenarios, we could anticipate snowmelt dates throughout the 21<sup>st</sup> century.

By the end of the century, we expect an earlier snowmelt by up to one month. Such an early melt will affect hydropower production, winter tourism in the Swiss Alps and will expose the alpine flora and soils to a higher frost risk with additional consequences on biogeochemical cycles.

## References

- Bader S, Fukutome S (2015) Milde und kalte Bergwinter [Mild and cold mountain winters]. *Fachbericht MeteoSchweiz* 254:1–10
- Baptist F, Flahaut C, Streb P, Choler P (2010a) No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. *Plant Biol* 12:755–764. doi: 10.1111/j.1438-8677.2009.00286.x
- Baptist F, Yoccoz NG, Choler P (2010b) Direct and indirect control by snow cover over decomposition in alpine tundra along a snowmelt gradient. *Plant Soil* 328:397–410. doi: 10.1007/s11104-009-0119-6
- Bartoń K (2019) MuMIn: Multi-Model Inference. R package version 1.43.15. <https://cran.r-project.org/package=MuMIn>
- Bavay M, Lehning M, Jonas T, Löwe H (2009) Simulations of future snow cover and discharge in Alpine headwater catchments. *Hydrol Process* 23:95–108. doi: 10.1002/hyp.7195
- Beniston M, Stoffel M, Giacomoni F, Farinotti D, Andreassen LM, Magnusson J, Coppola E, Fantini A, Eckert N, Naaim M, Hauck C, Huss M, Huwald H, Lehning M, Marty C, López-Moreno JI, Morán-Tejeda E, Morin S, Provenzale A, Rabatel A, Six D, Vincent C, Stötter J, Strasser U, Terzago S (2018) The European mountain cryosphere: A review of its current state, trends, and future challenges. *Cryosphere* 12:759–794
- Buchmann M, Begert M, Brönnimann S, Marty C (2020) Evaluating the robustness of snow climate indicators using a unique set of parallel snow measurement series. *Int J Climatol* 1–11. doi: 10.1002/joc.6863
- Ceppi P, Scherrer SC, Fischer AM, Appenzeller C (2012) Revisiting Swiss temperature trends 1959–2008. *Int J Climatol* 32:203–213. doi: 10.1002/joc.2260
- CH2018 Project Team (2018) CH2018 - Climate Scenarios for Switzerland. Natl. Cent. Clim. Serv.
- CH2018 (2018) CH2018 Climate change scenarios for Switzerland - Technical report, National Centre for Climate Services. Zurich, p271

- Cryer JD, Chan K-S (2008) Time series analysis with applications in R, 2nd edn. Springer Science+Business Media, LLC, New York, USA
- Edwards AC, Scalenghe R, Freppaz M (2007) Changes in the seasonal snow cover of alpine regions and its effect on soil processes: A review. *Quat Int* 162 & 163:172–181. doi: 10.1016/j.quaint.2006.10.027
- Essery R, Kim H, Wang L, Bartlett P, Boone A, Brutel-Vuilmet C, Burke E, Cuntz M, Decharme B, Dutra E, Fang X, Gusev Y, Hagemann S, Haverd V, Kontu A, Krinner G, Lafaysse M, Lejeune Y, Marke T, Marks D, Marty C, Menard C, Nasonova O, Nitta T, Pomeroy J, Schaedler G, Semenov V, Smirnova T, Swenson S, Turkov D, Wever N, Yuan H (2020) Snow cover duration trends observed at sites and predicted by multiple models. *Cryosph Discuss*. In press. doi: 10.5194/tc-2020-182
- Francon L, Corona C, Till-Bottraud I, Choler P, Carlson BZ, Charrier G, Améglio T, Morin S, Eckert N, Roussel E, Lopez-Saez J, Stoffel M (2020) Assessing the effects of earlier snow melt-out on alpine shrub growth: The sooner the better? *Ecol Indic* 115:1–13. doi: 10.1016/j.ecolind.2020.106455
- Freppaz M, Celi L, Marchelli M, Zanini E (2008) Snow removal and its influence on temperature and N dynamics in alpine soils (Vallée d’Aoste, northwest Italy). *J Plant Nutr Soil Sci* 171:672–680. doi: 10.1002/jpln.200700278
- Heide OM (2001) Photoperiodic control of dormancy in *Sedum telephium* and some other herbaceous perennial plants. *Physiol Plant* 113:332–337. doi: 10.1034/j.1399-3054.2001.1130305.x
- Hock R, Rasul G, Adler C, Cáceres B, Gruber S, Hirabayashi Y, Jachson M, Kääb A, Kang S, Kutuzov S, Milner A, Molau U, Morin S, Orlove B, Steltzer H (2019) High mountain areas. In: Pörtner H-O, Roberts DC, Masson-Delmotte V, et al. (eds) IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. In press. pp 131–202
- Hülber K, Winkler M, Grabherr G (2010) Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. *Funct Ecol* 24:245–252. doi: 10.1111/j.1365-2435.2009.01645.x
- IPCC (2013) Climate change 2013 The Physical Science Basis, Working group I contribution to 5th assessment report of the intergovernmental panel on climate change
- Jacob D, Petersen J, Eggert B, Alias A, Christensen OB, Bouwer LM, Braun A, Colette A, Déqué M, Georgievski G, Georgopoulou E, Gobiet A, Menut L, Nikulin G, Haensler A, Hempelmann N, Jones C, Keuler K, Kovats S, Kröner N, Kotlarski S, Kriegsmann A, Martin E, van Meijgaard E, Moseley C, Pfeifer S, Preuschmann S, Radermacher C, Radtke K, Rechid D, Rounsevell M, Samuelsson P, Somot S, Soussana JF, Teichmann C, Valentini R, Vautard R, Weber B, Yiou P (2014) EURO-CORDEX: New high-resolution climate change projections for European impact research. *Reg Environ Chang* 14:563–578. doi: 10.1007/s10113-013-0499-2
- Kawai Y, Kudo G (2018) Variations in ramet performance and the dynamics of an alpine evergreen herb, *Gentiana nipponica*, in different snowmelt conditions. *Am J Bot* 105:1813–1823. doi: 10.1002/ajb2.1186
- Keller F, Körner C (2003) The role of photoperiodism in alpine plant development. *Arctic, Antarct Alp Res* 35:361–368. doi: 10.1657/1523-0430(2003)035[0361:TROPIA]2.0.CO;2
- Klein G, Vitasse Y, Rixen C, Marty C, Rebetez M (2016) Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than later snow onset. *Clim Change* 139:637–549. doi: 10.1007/s10584-016-1806-y

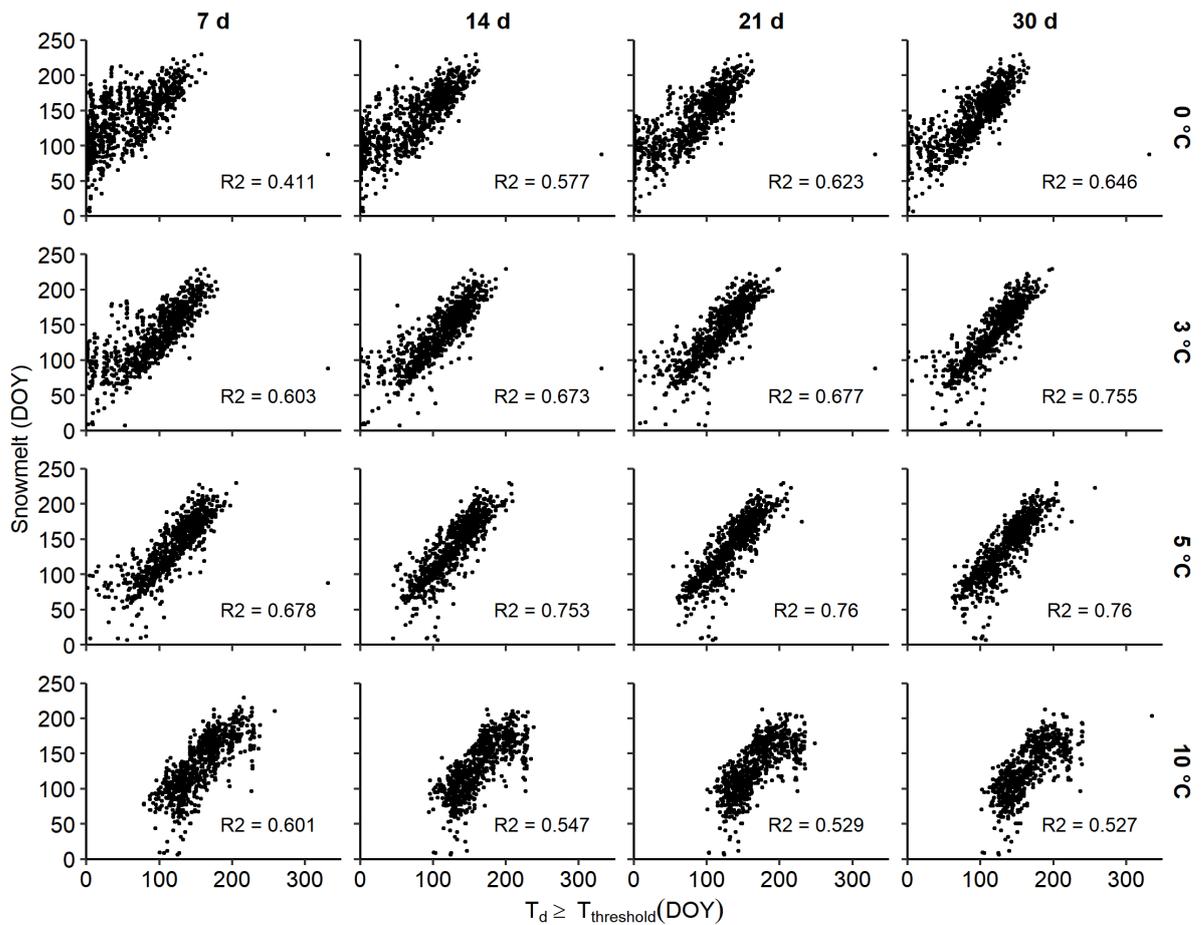
- Körner C (2003) Alpine plant life. Functional plant ecology of high mountain ecosystems, 2nd edn. Springer, Berlin Heidelberg. p 349
- Körner C, Riedl S, Keplinger T, Richter A, Wiesenbauer J, Schweingruber F, Hiltbrunner E (2019) Life at 0 °C: the biology of the alpine snowbed plant *Soldanella pusilla*. *Alp Bot* 129:63–80. doi: 10.1007/s00035-019-00220-8
- Laternser M, Schneebeli M (2003) Long-term snow climate trends of the Swiss Alps (1931-99). *Int J Climatol* 23:733–750. doi: 10.1002/joc.912
- Marty C (2008) Regime shift of snow days in Switzerland. *Geophys Res Lett* 35:L12501. doi: 10.1029/2008GL033998
- Marty C, Meister R (2012) Long-term snow and weather observations at Weissfluhjoch and its relation to other high-altitude observatories in the Alps. *Theor Appl Climatol* 110:573–583. doi: 10.1007/s00704-012-0584-3
- Marty C, Schlögl S, Bavay M, Lehning M (2017) How much can we save? Impact of different emission scenarios on future snow cover in the Alps. *Cryosph* 11:517–529. doi: 10.5194/tc-11-517-2017
- Morán-Tejeda E, López-Moreno JI, Beniston M (2013) The changing roles of temperature and precipitation on snowpack variability in Switzerland as a function of altitude. *Geophys Res Lett* 40:2131–2136. doi: 10.1002/grl.50463
- Musselman KN, Clark MP, Liu C, Ikeda K, Rasmussen R (2017) Slower snowmelt in a warmer world. *Nat Clim Chang* 7:214–219. doi: 10.1038/nclimate3225
- Pohlert T (2020) trend: non-parametric trend tests and change-point detection. R package version 1.1.2. <https://cran.r-project.org/package=trend>
- Prock S, Körner C (1996) A Cross-continental comparison of phenology, leaf dynamics and dry matter allocation in Arctic and temperate zone herbaceous plants from contrasting altitudes. *Ecol Bull* 45:93–103
- R Core Team (2019) R: A language and environment for statistical computing
- Rebetez M, Reinhard M (2008) Monthly air temperature trends in Switzerland 1901-2000 and 1975-2004. *Theor Appl Climatol* 91:27–34. doi: 10.1007/s00704-007-0296-2
- Reid PC, Hari RE, Beaugrand G, Livingstone DM, Marty C, Straile D, Barichivich J, Goberville E, Adrian R, Aono Y, Brown R, Foster J, Groisman P, Hélaouët P, Hsu HH, Kirby R, Knight J, Kraberg A, Li J, Lo TT, Myneni RB, North RP, Pounds JA, Sparks T, Stübi R, Tian Y, Wiltshire KH, Xiao D, Zhu Z (2016) Global impacts of the 1980s regime shift. *Glob Chang Biol* 22:682–703. doi: 10.1111/gcb.13106
- Saffioti C, Fischer EM, Scherrer SC, Knutti R (2016) Reconciling observed and modeled temperature and precipitation trends over Europe by adjusting for circulation variability. *Geophys Res Lett* 43:8189–8198. doi: 10.1002/2016GL069802
- Scherrer SC, Appenzeller C, Laternser M (2004) Trends in Swiss Alpine snow days: The role of local- and large-scale climate variability. *Geophys Res Lett* 31:L13215. doi: 10.1029/2004GL020255
- Scherrer SC, Wüthrich C, Croci-Maspoli M, Weingartner R, Appenzeller C (2013) Snow variability in the Swiss Alps 1864-2009. *Int J Climatol* 33:3162–3173. doi: 10.1002/joc.3653
- Schmucki E, Marty C, Fierz C, Weingartner R, Lehning M (2015a) Impact of climate change in Switzerland on socioeconomic snow indices. *Theor Appl Climatol* 127:875–889. doi: 10.1007/s00704-015-1676-7

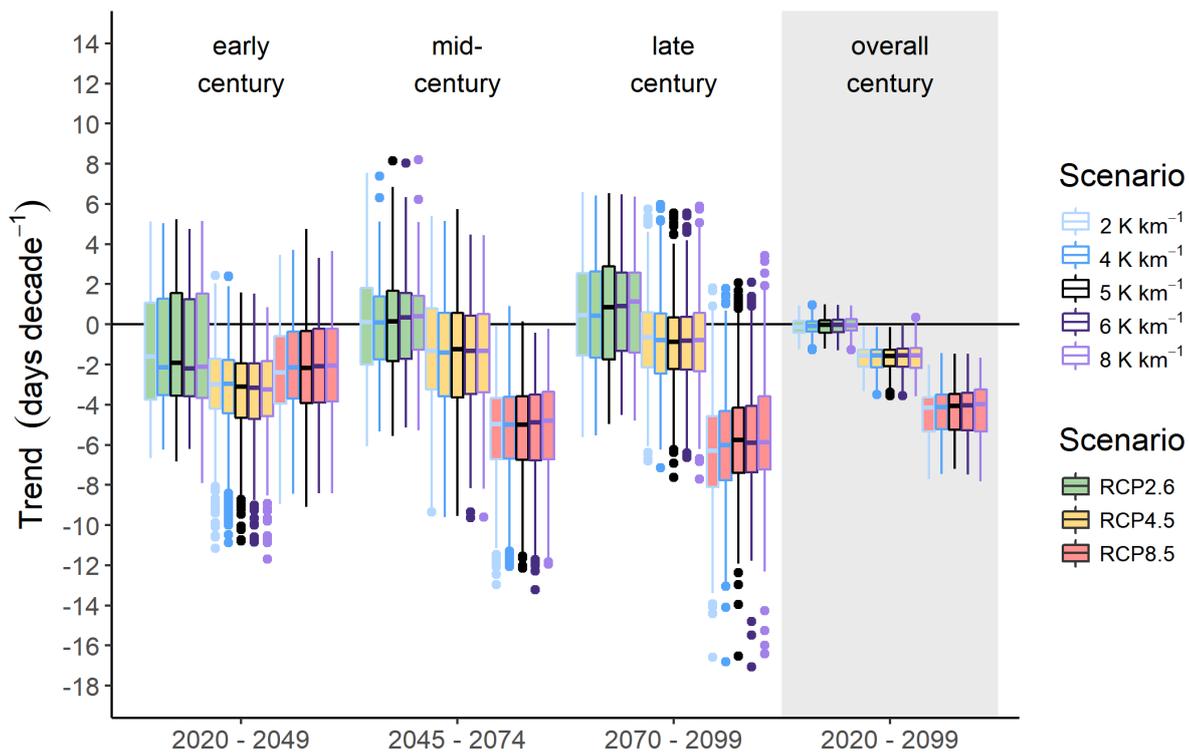
- Schmucki E, Marty C, Fierz C, Lehning M (2015b) Simulations of 21st century snow response to climate change in Switzerland from a set of RCMs. *Int J Climatol* 35:3262–3273. doi: 10.1002/joc.4205
- Sippel S, Fischer EM, Scherrer SC, Meinshausen N, Knutti R (2020) Late 1980s abrupt cold season temperature change in Europe consistent with circulation variability and long-term warming. *Environ Res Lett* Accepted:1–20. doi: 10.1088/1748-9326/ab86f2
- Steger C, Kotlarski S, Jonas T, Schär C (2013) Alpine snow cover in a changing climate: A regional climate model perspective. *Clim Dyn* 41:735–754. doi: 10.1007/s00382-012-1545-3
- Tonin R, Gerdol R, Tomaselli M, Petraglia A, Carbognani M, Wellstein C (2019) Intraspecific functional trait response to advanced snowmelt suggests increase of growth potential but decrease of seed production in snowbed plant species. *Front Plant Sci* 10:1–12. doi: 10.3389/fpls.2019.00289
- Westaway R (2000) Modelling the potential effects of climate change on the Grande Dixence hydro-electricity scheme, Switzerland. *Water Environ* 14:179–185
- Wipf S, Rixen C (2010) A review of snow manipulation experiments in arctic and alpine tundra ecosystems. *Polar Res* 29:95–109. doi: 10.1111/j.1751-8369.2010.00153.x
- Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Clim Change* 94:105–121. doi: 10.1007/s10584-009-9546-x

## Supplemental material for Chapter 1

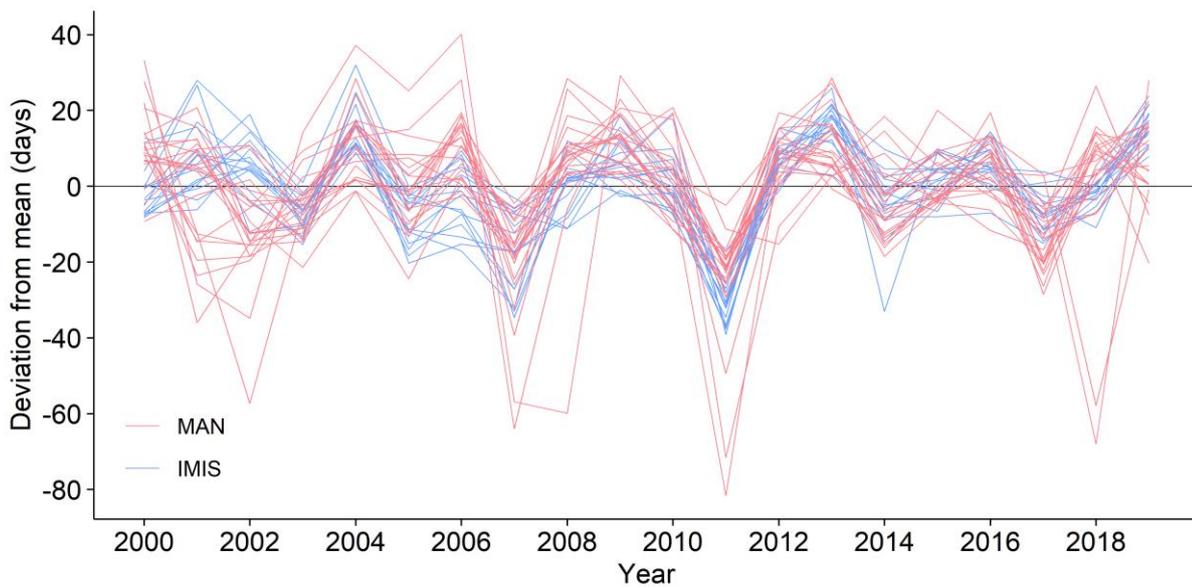
**Table S1.1** Stations with data gaps in snowmelt dates (years) and how these gaps were filled

Station	Years	Gap filling of snowmelt
1GB	1960	Derived from snow depth measurements
1MR	1960	Derived from snow depth measurements
2EN	1970	Derived from snow depth measurements
6RI	1958, 1970	Based on similar course of HS during these two years
GOS	2015	Derived from snow depth measurements
GRH	1975, 1979, 1991, 1993, 1995, 1997	Correlation with GUE
GTT	1954, 2012	Correlation with 1WE
GUE	1961, 1965, 1973	Derived from snow depth measurements
	2004 - 2014	Correlation with GRH

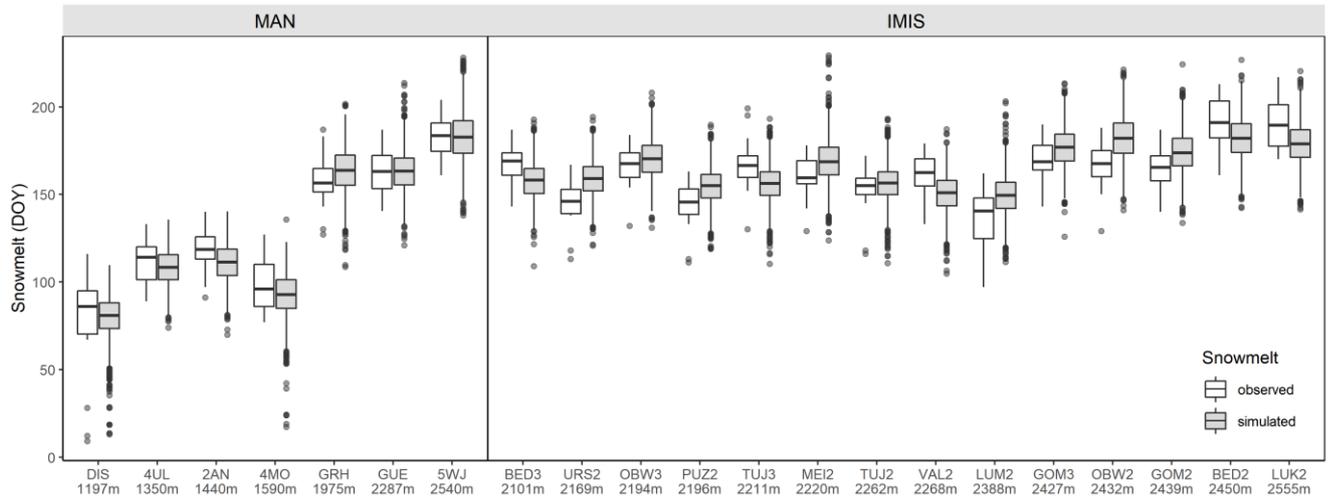
**Figure S1.1** Snowmelt date (DOY) in relation to the first day (DOY) when the mean air temperature of a running window (d: 7, 14, 21, 30 days; columns) reaches a temperature threshold ( $T$ : 0, 3, 5, 10 °C; rows) with the corresponding coefficient of determination  $R^2$



**Figure S1.2** Projected trends in snowmelt dates of 14 IMIS stations throughout the 21<sup>st</sup> century for the three emission scenarios RCP2.6, RCP4.5 and RCP8.5. In total 68 simulations basing on downscaled regional climate models: 12 for RCP2.6, 25 for RCP4.5, and 31 for RCP8.5. The colour of the whiskers indicates the lapse rate for air temperature used for correcting for elevational differences between the grid cells of climate change scenarios and the IMIS station. The coloured box contains 50% of all simulations per RCP scenario and time period



**Figure 1.3** Yearly deviation of snowmelt dates from the 10-year average (2000-2009) for manual 22 MAN (red) and 15 automatic IMIS (blue) stations



**Figure S1.4** Observed snowmelt (white boxplots) and simulated snowmelt based on the retrospective climate change scenarios (grey boxplots) for the reference period for the stations. The reference period for MAN stations is 1990 – 2019, for IMIS stations 2000 – 2019. Each boxplot contains all 68 simulations of three RCP scenarios for each year of the reference period (MAN: 30 x 68, IMIS: 20 x 68)





## Chapter 2 - Flowering phenology in alpine grassland strongly responds to shifts in snowmelt but weakly to summer drought

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### Keywords

Alps, climate change, growing season, high elevation, photoperiod, snow cover, survival analysis

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## Abstract

Alpine plants complete their seasonal phenological cycle during two to three snowfree months. Under climate change, snowmelt advances and the risk of summer droughts increases. Yet, photoperiodism may prevent alpine plants from benefiting from an earlier start of the growing season. To identify the drivers of flowering phenology in the seven main species of an alpine grassland, we experimentally shifted the snowmelt date through snow manipulations, and excluded precipitation during summer. With “time-to-event” models, we analysed the beginning of main flowering with respect to temperature sums, time after snowmelt, and calendar day (photoperiod).

We identified two phenology types: four species tracking snowmelt dates directly or with a certain lag set by temperature sums, including the dominant sedge *Carex curvula*, *Anthoxanthum alpinum*, *Helictotrichon versicolor*, and *Trifolium alpinum*, and three species tracking photoperiod: *Geum montanum*, *Leontodon helveticus* and *Potentilla aurea*. Photoperiodism did not manifest through specific daylength requirements but modulated the thermal sums at flowering. Hence, photoperiod delayed flowering after earlier snowmelt. The grass *A. alpinum* was the only one of seven species that clearly responded to drought by earlier and longer flowering.

The remarkably high importance of snowmelt dates for both phenology types suggests an earlier onset of flowering in a warmer climate, particularly for non-photoperiod sensitive species, with an increasing risk for freezing damages and potential disruptions of biotic interactions in the most frequent type of alpine grassland across the Alps. Consequentially, the distinct microclimate and species-specific responses to photoperiod challenge temperature-only based projections of climate warming effects on alpine plant species.

## Introduction

In alpine regions, the length of the growing season is determined by snow cover duration and alpine plant development is closely linked to snowmelt timing (Körner 2021). During recent decades, shifts in snow cover have been observed particularly below the treeline, but also for alpine and nival zones (Marty 2008; Scherrer *et al.* 2013; Klein *et al.* 2016; Hock *et al.* 2019). Further massive reductions in snow cover duration are predicted under ongoing and future climate change (Keller *et al.* 2005; Steger *et al.* 2013; Hock *et al.* 2019). Summer droughts are expected to occur more frequently and to be more severe (IPCC 2018), and may therefore limit alpine plant species that otherwise profit from an earlier growing season.

### *Photoperiodism*

Given the long-lasting snow cover, alpine plants have to complete their growth and reproduction very rapidly within a 10-12 weeks growing season. Besides bud preformation (Erschbamer *et al.* 1994; Meloche and Diggle 2001), mechanisms are required to precisely control plant phenology. About half of 23 species studied in the high alpine belt (2,600-3,200 m a.s.l) have displayed pronounced photoperiodism in the greenhouse (response to daylength, thus to photoperiod; Keller and Körner 2003). Photoperiodism prevents plant development during warm spells in late winter or early spring and facilitates synchronized flowering, presumably increasing reproductive success (Heide 2001; Keller and Körner 2003). Heide (1985, 1990, 1992, 2005; Heide *et al.* 1990) provided compelling evidence that photoperiod plays a decisive role in many arctic plant species. The significance of photoperiod has predominantly been studied in form of thresholds or long-day requirements (e.g., Heide 2001; Keller and Körner 2003). In the context of climatic change, photoperiodism may prevent species from benefiting from earlier snow melt. Species that are tightly linked to photoperiod cues, could have a competitive disadvantage over more non-photoperiod sensitive species. Wadgyamar *et al.* (2018) highlighted that the flowering phenology of six subalpine forbs has not advanced as rapidly as the snowmelt dates (1973-2016: one-week earlier snowmelt induced 3.5 to 5 days earlier flowering only).

However, *in situ* evidence for photoperiodism in the alpine belt is still scarce. Recently, several studies with transplanted montane and alpine plants at different elevations (common gardens) underline that plant species from higher elevation flowered earlier when brought to lower elevation with earlier snowmelt (Gugger *et al.* 2015), especially early-flowering species or graminoids seem to be more responsive to earlier snowmelt than late flowering species (Wadgyamar *et al.* 2018). Although common gardens have many advantages such as allowing a differentiation between genotypic and phenotypic acclimatisation, pre-cultivation of alpine plant species at lowland conditions (in the greenhouse) and commonly offering nutrient rich soil substrates or restricting rooting volumes by pots may affect plant performances and also phenological responses in common gardens.

In general, natural differences in photoperiod under variable snowmelt in the field are typically far smaller than those often applied in greenhouse and transplant experiments.

Furthermore, higher temperatures are expected to accelerate plant development in addition to photoperiod signals (Heide 1992). Without photoperiod control, temperature sums alone may drive plants to respond to early snowmelt, causing earlier flowering, but simultaneously increasing the risk of freezing damages.

The cascade of processes in a plant after the photoperiod threshold for flowering is passed, the interaction with temperature in particular, is not well understood. To predict future plant responses

to an earlier onset of the growing season such interactions between drivers have to be accounted for. Here, we aim at deciphering these interactions experimentally by manipulating the onset of the growing season by snow manipulation under alpine field conditions.

#### *The effect of snowmelt date and temperature on phenology*

A 31-year-long study in the Rocky Mountains revealed a close correlation of first flowering and snowmelt dates, provided snowmelt did not occur exceptionally early in the year (Inouye 2008). A tight coupling of plant development with snowmelt dates was also observed in other high elevation and high latitude ecosystems, which differed in daylength (e.g., Canaday and Fonda 1974; Ram *et al.* 1988; Wipf and Rixen 2010). For alpine plant species not assumed to be photoperiod sensitive, post-snowmelt temperatures were considered to control the phenology (e.g., Kudernatsch *et al.* 2008; Livensperger *et al.* 2016; warming with open-top chambers). Earlier attempts at identifying drivers of alpine plant phenology have already considered both, temperature and photoperiod, but have not addressed their potential interaction (Molau *et al.* 2005; Hülber *et al.* 2010).

When studying temperature effects on alpine plant species, it is important to account for the actual growing conditions of meristematic tissues. Given that the compressed, small stature of alpine plants creates a warmer microclimate, weather station data, as often used for phenological models, are not a reliable data source for temperatures that are driving alpine plant development (Scherrer and Körner 2010; Dietrich and Körner 2014; Körner and Hiltbrunner 2018).

#### *Summer drought*

Despite the typically positive water balance at high elevations in temperate mountains (Weingartner *et al.* 2007), recent heat waves and precipitation deficits in the Alps (2003, 2015, 2018) have shown that summer drought occurs above the upper treeline and plants have been spotted wilting (personal observations). In a low elevation grassland, drought both advanced flowering and prolonged flower duration by four days (Jentsch *et al.* 2009). Complete rain exclusion during 43 days in an otherwise very humid region increased the seed mass of plant species occurring at higher elevations, presumably promoting seedling recruitment in a calcareous grassland (Rosbakh *et al.* 2017). An experimental drought for 17 days reduced phytomass production in alpine grassland (de Boeck *et al.* 2016). Schmid *et al.* (2011) observed reductions of 12% to 35% in aboveground biomass of a similar grassland type under summer drought. None of these studies included phenological observations. Nevertheless, the combination of shifting snowmelt dates and summer drought may have a large impact on alpine grassland, in particular on developmental processes (phenology), with implications for biotic interactions and gene flow, as well as for future species distribution.

#### *Main objectives*

In this study, we aimed at identifying the drivers of flowering phenology and flower duration for the main plant species in a late successional alpine grassland and to explore how summer drought interferes with these drivers. To assess drivers and their interactions, we established a snow manipulation and rain exclusion experiment at 2,500 m a.s.l. This late successional grassland, dominated by *Carex curvula*, is the most widespread type of alpine grassland on siliceous bedrock in the European Alps (Oberdorfer 2001; Leuschner and Ellenberg 2017). We present a phenological dataset covering the three years 2016-2018, supplemented with detailed microclimatic data for the growing seasons.

As snowmelt commonly occurs around summer solstice at our field site, we hypothesize (1) that temperature after snowmelt plays a more crucial role for phenology than does photoperiod, with (2) an influence of photoperiod after exceptionally early snowmelt only. As soil moisture continuously decreases under ongoing drought, we expect (3) late flowering species to be significantly more affected by drought than early flowering species.

## Materials and Methods

### Site description

The study site is located at 2,500 m a.s.l. near the Furka pass in the Swiss central Alps (46° 33' 47" N, 8° 23' 28" E) in a late successional grassland on siliceous podsol. For an earlier site description and productivity data see Schappi and Korner (1996). The growing season lasts approximately three months with snowmelt usually occurring in June and senescence starting in the second half of August. Mean air temperatures during June, July and August are 6.0 °C, 8.7 °C and 8.3 °C (Furka pass, [www.alpfor.ch](http://www.alpfor.ch)). As a result of the continuous snowpack at the site, soils commonly do not freeze in winter. Summer precipitation amounts to ca. 400 mm (Jun-Aug, Furka pass). With an inclination of 10° the terrain is relatively flat for alpine terrain and well suited for an experiment with snow manipulations and summer drought. Most of the roots and the apical shoot meristems are located in the upper 5 cm of the soil profile and the mean rooting depth is around 20 cm (few roots down to 1 m depth). Besides the dominant sedge *Carex curvula* All., other frequently occurring species are the grasses *Anthoxanthum alpinum* . Love & D. Love, *Helictotrichon versicolor* (Vill.) Pilg. and *Poa alpina* L., the forbs *Geum montanum* L., *Leontodon helveticus* Merat, *Potentilla aurea* L., *Sibbaldia procumbens* L. and *Soldanella pusilla* Baumg., and the N<sub>2</sub>-fixing forb *Trifolium alpinum* L. (species nomenclature according to Lauber *et al.* 2018). Fruticose lichens (*Cetraria islandica* L. and various *Caldonia* species) are abundant in this alpine grassland. However, as the age of the lichens cannot be determined and lichens may dry out for longer periods, we did not include them in the field observations.

### Snow manipulation and summer drought

We implemented all combinations of summer drought (control, moderate – 5-wk drought spanning the main period for the above-ground biomass production, intense –10.5-wk drought covering almost the entire growing season) and snow manipulations (control, addition, removal) in a fully factorial experimental design. We had 45 parcels (2 x 2.5 m), organized in five replicated blocks. In each block, the nine parcels were randomly assigned to one fixed treatment combination. To avoid any boundary effects of the drought treatment, we defined a central plot (1 x 1 m) within each parcel.

We conducted the snow manipulations in late spring 2016–2018 (beginning of June 2016, end of May 2017, first half of June 2018), two to three weeks before natural snowmelt (Figure 4.1). In 2016 and 2017 we decreased the snow depth from roughly 1 m to 0.5 m to achieve earlier snowmelt, and we increased the snow depth to 2.2–2.5 m to delay snowmelt. An unstable weather period in 2018 postponed the snow manipulation, so that the mean snow depth was only 0.5 m, thinner than desired for the treatment. We therefore removed snow down to 0.3 m and added it up to 0.5–0.7 m, depending on snow availability. Then, because of the lower snow depth on the snow addition parcels, we covered the snow addition parcels with a white, water permeable fleece (Datex KN25, Fritz Landolt AG, CH), which was removed after ten days when snow height was 0.3 m.

We applied the drought treatments using rainout shelters, starting directly after snowmelt: on June 16<sup>th</sup>, 2017 and on July 2<sup>nd</sup>, 2018 (no drought treatment in the year 2016).

The basal area of the shelters was 2.5x 3 m, thus, they were 0.5 m larger than the parcels in either direction. The tent-like shelters had a ridge height of 1.2 m, with both long edges reaching down to 10 cm above the ground and covered by UV-B permeable foil (Lumisol AF clear, Hortuna AG, CH). The triangular openings of the short sides were oriented in the main wind direction (W-E), ensuring a constant air flow to minimize microclimatic effects. Wooden strips at both long sides of the shelter drained the excluded rainwater outside the lower end of the parcel. These rainout shelters were constructed to withstand harsh alpine weather conditions and have already been successfully implemented for a drought experiment (Schmid *et al.* 2011, photo of rainout shelter in the Figure 2.1).

Temperature sensors in the centre of each plot (HOBO UTBI-001 TidbiT v2 Temp, Onset, US, 1-h measurement intervals) measured the soil temperature adjacent to most alpine plants' meristems (3-4 cm depth). Diurnal temperature fluctuations after snowmelt revealed exact snowmelt dates within each plot. We additionally used the soil temperatures for assessing temperature effects of rainout shelters (day- and night-time effects separated: 11 a.m.-10 p.m. and 11 p.m.-10 a.m. These 12-hour intervals consider daily minima and maxima of soil temperatures, lagging two hours behind air temperatures. During the growing seasons 2017 and 2018, every 10 minutes two weather stations (Vantage Pro2, Davis Instruments Corp., USA) recorded precipitation, global radiation and air temperatures at 1.5 m above ground. Surface temperatures were measured with an IR thermal camera (VarioCAM®, Infratec, Dresden, GER). Thermograms were taken in each plot on six sunny days with all rainout shelters removed (two times in 2017, four times in 2018) from a distance of 180 cm southwards of the plots at an angle that covered the whole plot. Pixel-based temperatures were extracted using the software IRBIS 2.20 (Infratec, Dresden, GER; temperatures are shown in Figure S2.1 and Table S2.1).

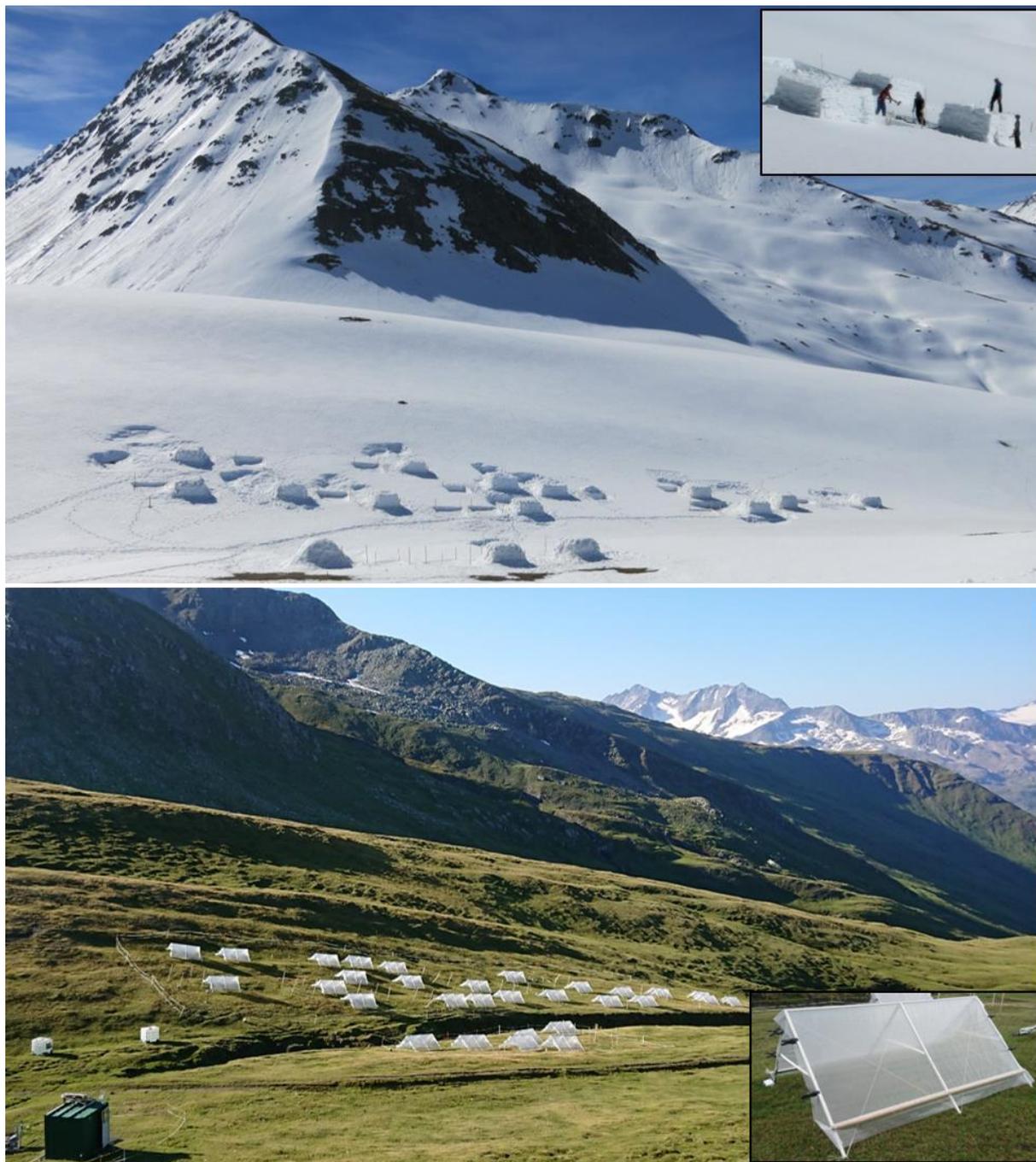
We manually measured the soil moisture of the top 5 cm (Theta probe ML2x, Delta-T Devices, UK), with a one to two weeks interval. For assessing the drought effect in both years, we averaged the soil moisture values over five separate time periods as rainout shelters were immediately installed after snowmelt and therefore differed in the date between the two years (N indicates the number of measuring campaigns during the corresponding period). Two time periods with all rainout shelters installed (moderate and intense drought, 1<sup>st</sup> and 2<sup>nd</sup> half), two time periods during intense drought (1<sup>st</sup> and 2<sup>nd</sup> half), and one after the removal of all rainout shelters. Eight soil moisture retention curves (pF curves, pF as the log<sub>10</sub> of the matrix potential) served as a reference for the actual drought effect (10 and 30 cm soil depth, measured with a HYPROP 2, METER Environment/UMS, GER). The growing season 2018 was exceptionally dry and we observed wilting adjacent to our study site, therefore, we watered the controls twice (1<sup>st</sup> and 28<sup>th</sup> of August), with 17 Lm<sup>-2</sup> each, to prevent any drought damages in the controls.

## Phenology

We assessed phenology twice a week directly after snowmelt, weekly throughout the main season, and biweekly at the end of the season (after flower senescence). This resulted in 7, 12 and 10 phenology assessments in the years 2016, 2017 and 2018, respectively. For each plot and each species growing on it, we determined its phenological stage. We characterized main flowering as the state when the majority ( $\geq 50\%$ ) of flowering individuals on a plot had fully open flowers, and clearly visible open anthers and stigmas in case of sedge and grass species. We assessed flower senescence when the majority of flowering individuals had dried or fallen off petals or dried and

broken off anthers for the graminoids. We then defined the transition to main flowering (TMF) as the start date of main flowering, and the flower duration as the time span until flower senescence. TMF was used for the analysis instead of the transition to earliest flowering because of its distinct signal at plant species level (e.g., CaraDonna *et al.* 2014).

Although we selected the most abundant species only, not all of these occurred in each plot. Dominant graminoids (*C. curvula*, *H. versicolor*) had often more than 50 individuals per plot, while forb species were much less abundant (6-20 individuals per plot). We therefore restricted our analysis to species that occurred at least three times per implemented treatment combination (snow and drought treatments) in all three years ( $n = 3-5$ ). These were the sedge *C. curvula*, the



**Figure 2.1** Snow manipulations and rainout shelters at the field site at 2,500 m a.s.l. in 2017. The insert with snow manipulations was retrieved from <https://www.webcam-4insiders.com/de/Oberwald/15221-Oberwald.php> (on-site webcam)

grasses *A. alpinum* and *H. versicolor* as well as the forbs *G. montanum*, *L. helveticus*, *P. aurea*, and *T. alpinum*. In 2016, flowering was not recorded in *A. alpinum*.

### Drivers for flowering phenology and interval censoring

We differentiated between flowering phenology driven by (1) snowmelt or by snowmelt and the subsequent temperature regime, and (2) photoperiod (or an interaction between photoperiod and temperature). A special case of (1) would be a fully opportunistic plant species that starts flowering immediately after snowmelt with concurrent temperature allowing for a delay of only a few days till TMF. For the transition to main flowering (TMF) we thus considered (1) the day of the year (DOY) with its specific *photoperiod* (PP), (2) the *time* in days elapsed since snowmelt (DSM), and (3) *temperature*, expressed by thermal sums (TS, °h  $\geq 0^\circ\text{C}$  or  $\geq 5^\circ\text{C}$ ) measured close to apical meristems (at 3-4 cm soil depth; TS  $\geq 5^\circ\text{C}$  are presented in the Figure S2.1 only). DSM and TS are highly correlated across the whole growing season, but not necessarily during the first few days after snowmelt. Especially for early flowering species, these temperatures at the very start of the growing season may be decisive for TMF and therefore, both drivers were considered here, but analysed separately. From the phenology census, we identified the interval of the transition for TMF and flower senescence, respectively. The last observation prior to TMF corresponds to the lower interval boundary and the first observation of main flowering represents the upper interval boundary after the transition. For these intervals with the phenological shift, we have continuous records of the three potential drivers (DOY / PP, DSM, TS).

### Data analysis

#### *Drivers of TMF*

For each driver and each plant species separately, we analysed whether snow manipulation, summer drought or the different years led to a significant shift (delay / advance) of TMF. We used time-to-event analysis (R package *survival* v2.43.3, Therneau 2015) with our census observations to delineate TMF. Time-to-event regression is specifically designed for situations when only the interval of an event occurrence is known but not its exact time. Here, “event” refers to a phenological transition (TMF, flower senescence), and “time” denotes a phenological driver (DOY / PP, DSM, TS).

The so-called hazard function describes the probability of TMF to occur at time  $x$  and the corresponding survival curve provides the probability of the phenological transition to have already occurred by the time  $x$  (Klein and Moeschberger 2003). With the time-to-event regression, we fit a parametrical hazard function to the interval censored data. For each driver, each plant species and the two transitions, we tested three parametric distributions (exponential, Weibull, and log-logistic) and the best fit was chosen based on the log-likelihood. Additionally, we compared parametric to non-parametric stepwise models, and we graphically analysed response residuals. For each treatment and each year, we determined TMF at the driver's value with a 50% probability for individuals within plots to have transitioned ( $p50$ ). We calculated the TMF's  $p50$  values and their confidence intervals for each treatment combination in each year.

As summer drought was implemented in 2017 and 2018 only, we tested its effect for these two years separately (model with drought, snow manipulations and years,  $n = 3-5$ ). In case of a significant drought effect, only parcels without drought treatments were used for the further analysis of the snow treatments across all three years (2016-2018). For all analyses, we allowed twofold interactions, as higher number of interactions could not be interpreted in an ecologically reasonable manner for the given set-up. Significant treatment and year effects were assessed using type III

ANOVA. Because TMF occurred before the end of the moderate drought treatment, we averaged the values for the moderate and intense drought treatments. We present absolute values, but the drivers for TMF were standardized to values between 0 and 1 to allow direct comparisons among drivers. The predictive power of a driver was judged by its degree of concurrence with the observed onset of TMF. The best fitting driver was identified by a very small difference between the earliest and the latest onset of a phenological shift across experimental treatments in all three years (standardized range of TMF).

#### *Photoperiod dependent temperature sums*

In addition to the treatment effects, we investigated the linear relation of TS ( $^{\circ}\text{h} \geq 0^{\circ}\text{C}$ ) at TMF and snowmelt dates (with its respective photoperiod) for each species, again with time-to-event analysis, using a gaussian hazard distribution. For those species with a drought effect in the prior analysis, we also tested the response to drought, allowing for the interaction of drought and snowmelt dates.

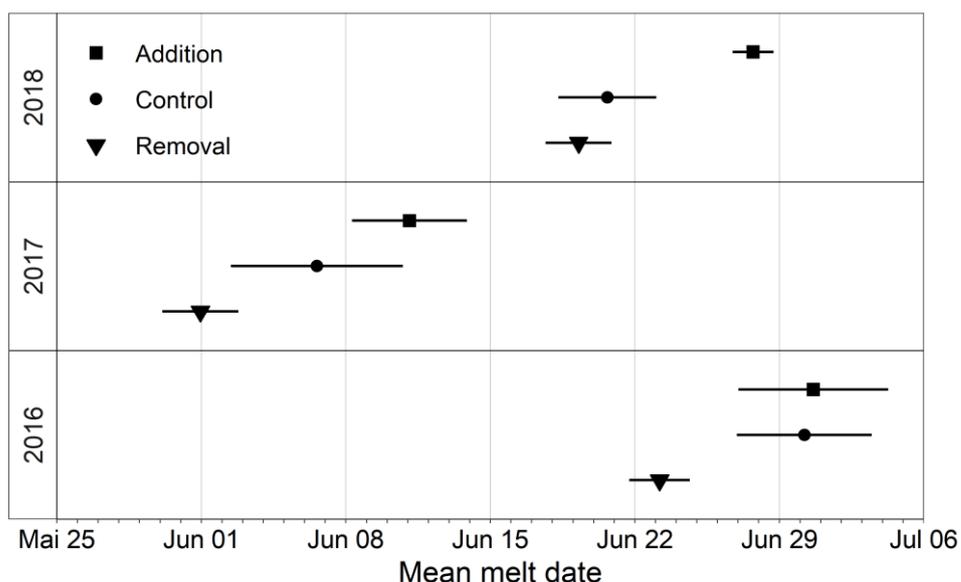
#### *Flower duration*

We assessed the flower duration as the time difference between TMF and the transition to flower senescence (both  $p50$  values).  $p50$  values were extracted from survival models, based on the driver days since snowmelt (DSM). Particularly later in the growing season, DSM and TS are highly correlated, and therefore, we here report flower durations expressed in DSM (days) but not in TS ( $^{\circ}\text{h}$ ). For flower duration we considered 2017 and 2018 only. The difference in natural snowmelt dates among the two years was far larger than what we achieved through snow manipulations. Thus, for flower duration, we accounted for differences between years and for the effect of drought, but not for the effect of snow manipulation. Thereof, we derived one flower duration per treatment combination and year. This resulted in a replicate of  $n = 3$  per drought treatment and year. We applied stepwise backwards model selection to the full model with interaction effects between species, years, and drought treatment. Contrasts were calculated through Tukey HSD post hoc comparisons (R package *emmeans* v1.4.2., Lenth *et al.* 2019). All analyses were performed with the statistical software *R-3.5.2* (R Core Team 2019).

## Results

### **Snow manipulation and snowmelt dates**

2016 was a relatively normal year with respect to snow cover and snowmelt date (Figure 2.2; compared to the data for the 2013-2020 period from the Furka weather station). Very little snow in the winter 2017 and an exceptionally warm spring led snowmelt to occur 24 days earlier than in the previous year, and 14 days earlier than in 2018. Snow manipulation in 2016 caused a nine days earlier snowmelt (snow removal) and a delay of one day only through snow addition. In 2017, snow removal advanced melt by six days and snow addition delayed it by four days. After a period with thunderstorms in spring 2018, snow manipulation was late and the combination of snow addition and fleece postponed snowmelt by six days, while the removal of snow from an



**Figure 2.2** Snowmelt date (mean  $\pm$  sd) of three consecutive years (2016-2018) with snow manipulation (see Figure 2.1)

already thin snowpack advanced snowmelt by two days only. Across all three years with snow manipulations, the range of snowmelt dates covered 38 days.

### Drought treatment and microclimatic effects

The drought treatments (moderate and intense) during the growing seasons 2017 and 2018 successfully reduced soil volumetric water contents (Table 2.1). Compared to the relatively normal summer precipitation in 2017 (+17% compared to the 2013-2016 mean for June-August), the 2018 growing season was very dry (-40% compared to 2013-2016) and temporarily, soil moisture in the controls of 2018 was lower than in the extreme drought treatment of 2017. Throughout the second half of the moderate drought treatment, soil moisture was on average 7.8 vol% (2017) and 7.3 vol % (2018) lower than in the control parcels. During the second half of the intense drought treatment, soil moisture was 15.2 vol% (2017) and 10.9 vol% (2018) lower than in controls, respectively. Mean soil moisture values did not drop below the permanent wilting point of 10.1 vol% (derived of eight pF curves at 10 cm soil depth; 8.8 vol% at 30 cm soil depth), but in single parcels soil moisture reached these values. After termination of the moderate drought treatment, average soil moisture values recovered to values in the range of the control parcels. Our weekly assessments showed that the snow manipulations did not affect the soil water contents beyond two weeks after the start of the drought treatment in 2017, and three weeks in 2018 (data not shown).

The rainout shelters induced slightly higher soil temperatures (0.3-1.4 K, Table 2.1), because of the inhibition of radiative cooling during night (0.1-0.4 K for the period with the intense drought treatment). Further, an increased warming effect under intense drought compared to moderate drought indicated less evaporative cooling under extreme drought. The overall soil temperature increase under rainout shelters amounted to 0.9 K.

Surface temperatures (thermal imaging) at single, sunny days (rain-out shelters briefly removed) were typically higher under experimental drought (up to 3.9 K under intense drought), pointing to stomatal closures and elevated sensible heat fluxes from leaves and soil surface (Figure S2.1 and Table S2.1).

**Table 2.1** Soil moisture (mean  $\pm$  sd) in the topsoil (0-5 cm, manually measured) of plots with moderate and intense drought during selected time periods 2017 and 2018 (n = 5 per treatment, 5 measuring points each) and soil temperature (mean  $\pm$  sd) in 3-4 cm depth (continuous measurements). N indicates the number of soil moisture measuring campaigns during the corresponding time period

Time period	Drought	Soil moisture (vol%)				Soil temperature (°C)			
		2017		2018		2017		2018	
			N		N	(day)	(night)	(day)	(night)
Mod. drought	control	32.2 $\pm$ 4.6	2	24.7 $\pm$ 4.4	2	16.1 $\pm$ 3.9	10.7 $\pm$ 2.4	16.3 $\pm$ 2.7	10.9 $\pm$ 1.4
1 <sup>st</sup> half	moderate	24.4 $\pm$ 6.2		19.5 $\pm$ 6.1		16.1 $\pm$ 3.6	11.5 $\pm$ 2.5	16.4 $\pm$ 2.5	11.7 $\pm$ 1.3
	intense	25.4 $\pm$ 5.7		20.2 $\pm$ 5.2		16.4 $\pm$ 3.8	11.5 $\pm$ 2.5	16.6 $\pm$ 2.6	11.8 $\pm$ 1.4
Mod. drought 2 <sup>nd</sup> half	control	30.0 $\pm$ 6.7		20.9 $\pm$ 5.4		15.2 $\pm$ 3.6	11.2 $\pm$ 2.1	17.0 $\pm$ 3.4	12.1 $\pm$ 1.8
	moderate	22.2 $\pm$ 5.8	4	13.6 $\pm$ 4.6	4	15.3 $\pm$ 3.4	11.9 $\pm$ 2.0	17.4 $\pm$ 3.3	13.1 $\pm$ 1.9
	intense	22.2 $\pm$ 5.9		13.9 $\pm$ 4.8		15.6 $\pm$ 3.5	11.9 $\pm$ 2.0	17.8 $\pm$ 3.4	13.3 $\pm$ 1.8
Intense drought 1 <sup>st</sup> half	control	34.0 $\pm$ 3.5		29.1 $\pm$ 5.5		14.4 $\pm$ 3.7	11.2 $\pm$ 1.9	15.5 $\pm$ 2.6	11.5 $\pm$ 1.2
	moderate	27.6 $\pm$ 5.8	1	21.1 $\pm$ 5.8	2	14.4 $\pm$ 3.8	11.0 $\pm$ 1.9	15.6 $\pm$ 2.7	11.4 $\pm$ 1.4
	intense	21.4 $\pm$ 5.8		15.2 $\pm$ 6.5		15.0 $\pm$ 3.1	12.0 $\pm$ 1.8	16.4 $\pm$ 2.6	12.5 $\pm$ 1.2
Intense drought 2 <sup>nd</sup> half	control	38.3 $\pm$ 4.4		25.1 $\pm$ 3.9		14.7 $\pm$ 3.2	10.1 $\pm$ 2.0	13.0 $\pm$ 2.7	9.3 $\pm$ 1.7
	moderate	35.0 $\pm$ 4.8	1	19.8 $\pm$ 4.5	2	14.8 $\pm$ 3.3	10.0 $\pm$ 2.0	13.0 $\pm$ 2.8	9.2 $\pm$ 1.7
	intense	23.1 $\pm$ 5.8		14.2 $\pm$ 4.9		15.7 $\pm$ 2.6	11.5 $\pm$ 1.7	13.8 $\pm$ 2.9	10.2 $\pm$ 1.7
After drought	control	22.6 $\pm$ 3.4		29.2 $\pm$ 3.7		8.3 $\pm$ 4.8	6.0 $\pm$ 3.5	13.9 $\pm$ 2.5	9.6 $\pm$ 1.3
	moderate	21.1 $\pm$ 4.0	1	25.8 $\pm$ 3.8	1	8.5 $\pm$ 4.9	6.1 $\pm$ 3.5	14.1 $\pm$ 2.6	9.5 $\pm$ 1.4
	intense	17.1 $\pm$ 3.3		20.6 $\pm$ 5.5		8.4 $\pm$ 5.0	6.0 $\pm$ 3.6	14.7 $\pm$ 3.1	9.6 $\pm$ 1.6

### Transition to main flowering (TMF)

The early snowmelt in 2017 induced early TMF in all species. Correspondingly, snow removal consistently induced an earlier, snow addition a later TMF in all species (DOY in Figure 2.3). Thus, no critical threshold in photoperiod could be observed. Nevertheless, we identified two groups of species, differing in their responsiveness to early snowmelt dates. The early snowmelt in 2017 (24 days earlier) advanced flowering by 20-24 days in *C. curvula*, *H. versicolor* and *T. alpinum* (no records for *A. alpinum* in 2016), indicating that TMF of this group of species is driven by the snowmelt date and the subsequent temperature regime. In a second, less responsive group, consisting of the forbs *G. montanum*, *L. helveticus* and *P. aurea*, flowering set in only 10 to 13 days earlier in 2017.

The driver DOY / PP consistently exhibited the broadest variation across all years and snow manipulations, whereas DSM and TS were always less variable (smaller horizontal grey bars in Figure 2.3). Without snow manipulation, DSM at TMF only varied by four days for the species *C. curvula*, *A. alpinum*, *H. versicolor* and *T. alpinum*, but by 7 to 13 days for *G. montanum*, *L. helveticus* and *P. aurea*. Thus, these results suggest that within the observational period of our study, DSM and TS exerted a substantially larger effect than DOY / PP, even in a year with exceptionally early melt and additional snow removal. In the following, we present the best fitting driver for TMF for each species of the two groups (Table 2.2).

### Temperature sums and days since snowmelt at the transition to main flowering

TMF in *C. curvula* was characterized by very similar TS (between 2,300 to 3,400 °h  $\geq$  0 °C) across years and snow manipulations (Table 2.2). DSM ranged between 9 and 15 days, but the total range of TMF (scaled) for TS was 45% smaller than for DSM. In control plots, *C. curvula*

**Table 2.2** *Best fitting driver* for TMF (transition to main flowering) of each plant species (2016-2018). Left: Thermal sums accumulated at TMF and days since snowmelt at TMF on controls (derived from time-to-event models,  $n = 3-5$ ). Values following snow removal (snow rem.), snow addition (snow add.) and drought are shown as difference to the control (units according to the driver). The difference of the drought treatment to the control is averaged over snow treatments. Right: test statistics (LR  $X^2$ ) for explaining variables for TMF (bold p-values indicate statistically significant differences). Abbreviation D: drought treatment, Y: year

Species	Best fitting driver	Y	TMF in control	Difference to control			Expl. Var	LR $X^2$ (df)	p-value	Expl. Var	LR $X^2$ (df)	p-value
				rem.	add.	D						
<i>Sedge</i>												
<i>C. curvula</i>	TS (°h)	2016	2,900	500	-100		S	11.27(2)	<0.01	D	2.23(1)	0.14
		2017	2,700	600	-300	500	Y	10.20(2)	0.01	D×S	3.67(2)	0.16
		2018	2,300	300	0	200	S×Y	1.39(4)	0.85	D×Y	1.58(1)	0.21
<i>Grasses</i>												
<i>A. alpinum</i>	DSM (days)	2016	-	-	-		S	2.14(2)	0.34	D	14.57(1)	<0.01
		2017	29	0	-2	-5	Y	0.06(1)	0.80	D×S	1.59(2)	0.45
		2018	29	-3	0	-4	S×Y	2.86(2)	0.24	D×Y	0.35(1)	0.55
<i>H. versicolor</i>	DSM (days)	2016	42	1	3		S	3.40(2)	0.18	D	0.13(1)	0.71
		2017	46	4	-4	2	Y	3.81(2)	0.15	D×S	2.43(2)	0.30
		2018	44	2	1	-1	S×Y	10.09(4)	0.04	D×Y	0.70(1)	0.40
<i>Forbs</i>												
<i>G. montanum</i>	TS (°h)	2016	3,200	1,000	300		S	5.65(2)	0.06	D	2.48(1)	0.12
		2017	5,500	100	-100	-200	Y	59.21(2)	<0.01	D×S	1.59(2)	0.45
		2018	5,200	300	-300	-500	S×Y	3.40(4)	0.46	D×Y	0.47(1)	0.49
<i>L. helveticus</i>	DSM (days)	2016	33	2	2		S	0.01(2)	0.01	D	1.70(1)	0.19
		2017	43	3	0	-1	Y	92.67(2)	<0.01	D×S	0.43(2)	0.81
		2018	36	1	-4	-2	S×Y	3.74(4)	0.05	D×Y	0.56(1)	0.46
<i>P. aurea</i>	TS (°h)	2016	6,300	300	1100		S	0.09(2)	0.96	D	0.45(1)	0.50
		2017	9,900	-900	-700	800	Y	28.57(2)	<0.01	D×S	0.20(2)	0.90
		2018	9,900	100	-700	-400	S×Y	6.05(4)	0.2	D×Y	3.62(1)	0.06
<i>T. alpinum</i>	TS (°h)	2016	9,600	1,400	-300		S	6.97(2)	0.03	D	3.13(1)	0.08
		2017	10,900	-300	1000	-600	Y	0.74(2)	0.69	D×S	0.36(2)	0.83
		2018	10,200	1,000	1300	-800	S×Y	2.56(4)	0.69	D×Y	0.08(1)	0.77

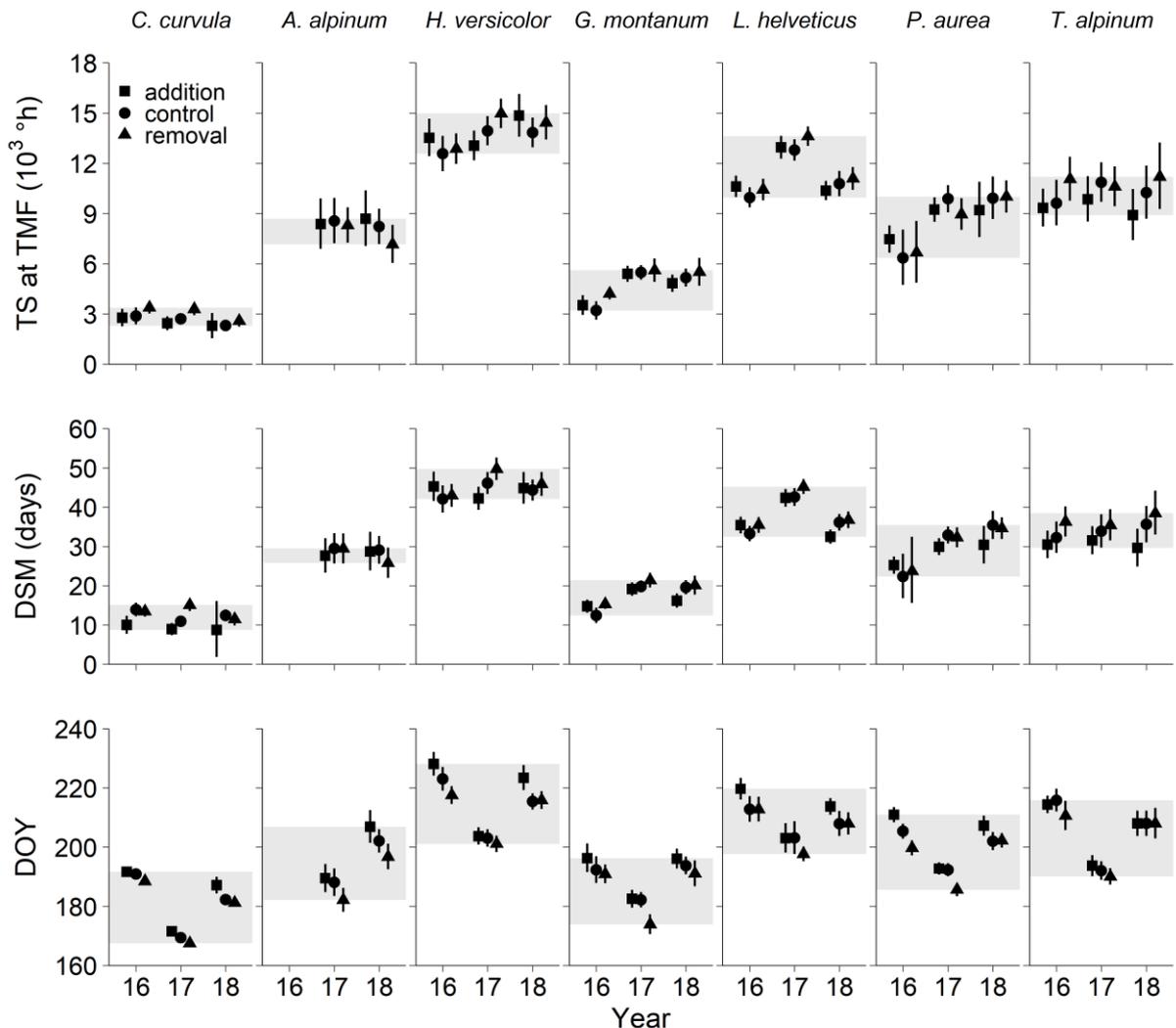
started flowering after accumulating 2,300 °h to 2,900 °h, with lowest values in 2018. Significant differences between years and snow manipulations (Table 2.2) were slightly smaller than TS typically accumulated during two average days in July (ca. 600 °h  $\geq$  0 °C day<sup>-1</sup>). This dominant sedge flowers very quickly after snowmelt and thus, represents a fully opportunistic flowering behaviour with respect to snowmelt date.

Similarly, but not as extreme as in *C. curvula*, for *T. alpinum*, TS was the best describing driver for TMF and compared to DSM, the range of TS at TMF was 15% smaller. *T. alpinum*'s TMF started at 10,200 °h on control plots without any significant differences between years. Snow manipulation significantly influenced TS at the TMF ( $p = 0.03$ ), with a delay after snow removal (+900 °h) and acceleration following snow addition (-700 °h). This had a slight compensatory effect within years, increasing the temporal synchronization of flowering (Figure 2.3). Nevertheless,

flowering after snow removal started up to five days earlier than on control plots. TS at TMF did not increase after snow removal in the early melt year 2017.

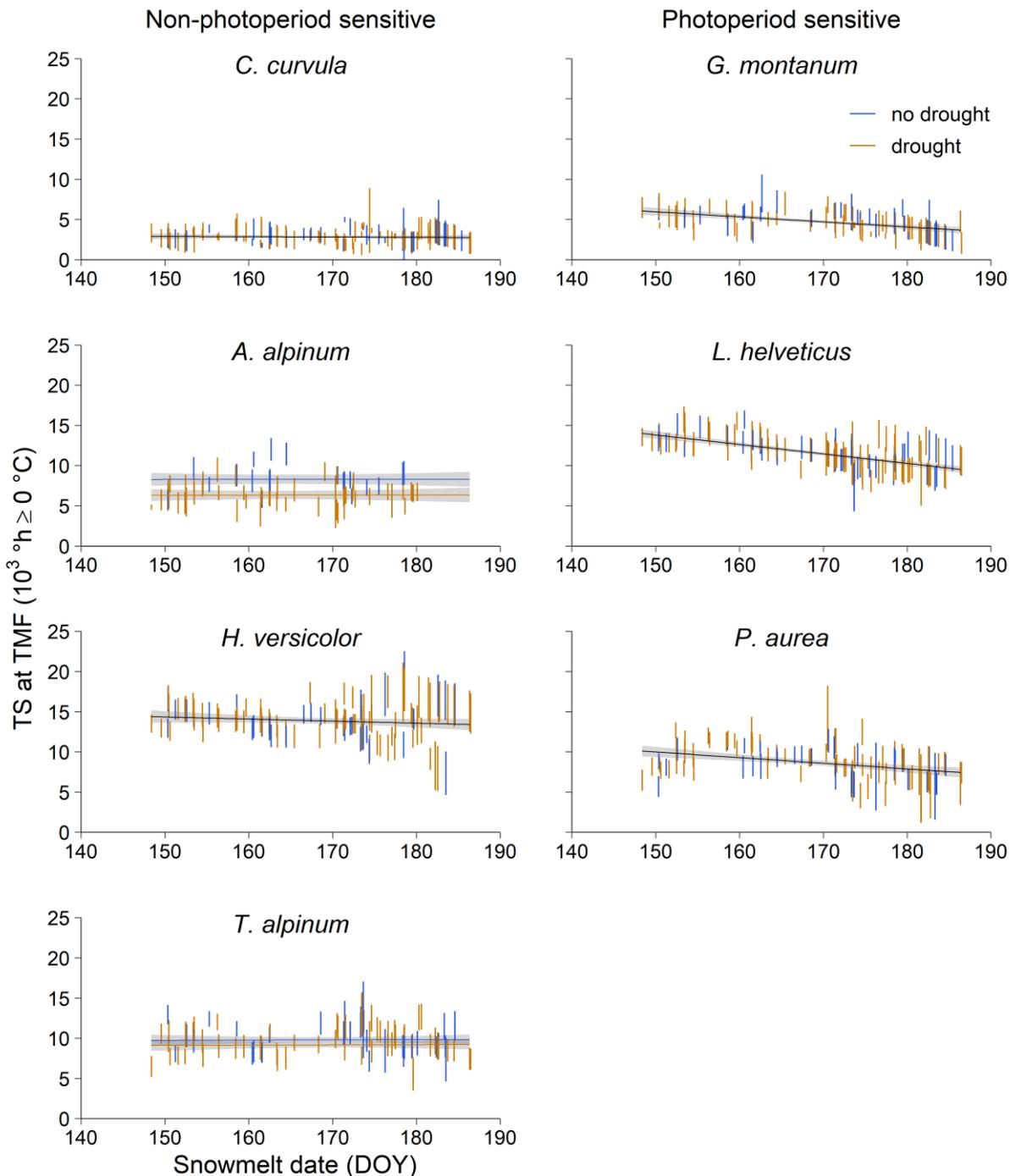
For *H. versicolor*, TS and DSM predicted the TMF equally well (2% difference in the range of TMF between the two drivers). Following natural snowmelt, it took *H. versicolor* 42 to 46 days to start flowering. Across all years, snow manipulations increased DSM by one to four days, except for snow addition in 2017, which accelerated TMF by four days compared to the control (interaction between snow manipulation and years,  $p = 0.04$ ). The same pattern was observed for the driver TS (Figure 2.3). TMF in *A. alpinum* on average occurred 28 days after snowmelt without any significant differences between years nor snow manipulations and with very a similar course for TS.

In contrast to the species above, TMF of *L. helveticus* showed large differences in both TS and DSM among years and snow manipulations (Figure 2.3). TMF started 33 (2016) to 43 (2017) days after natural snowmelt ( $p_{\text{year}} < 0.01$ ). Snow removal prolonged the time between snowmelt and flowering by 0.5 to 2.5 days, while snow addition caused contrasting responses among years (snow manipulation:  $p = 0.01$ , snow manipulation  $\times$  year interaction:  $p = 0.05$ , Table 2.2). The same pattern was observed for the driver TS (Figure 2.3). For *G. montanum* and *P. aurea*, the



**Figure 2.3** TMF for the three drivers DOY, DSM and TS ( $^{\circ}\text{h} \geq 0 \text{ }^{\circ}\text{C}$ ) of each plant species in 2016 – 2018 (DOY: day of the year, DSM: days since snowmelt, TS: temperature sum). Error bars represent 95% confidence intervals of TMF ( $n = 3\text{-}5$ ). Grey bars indicate the range of the driver at the TMF (earliest vs. latest TMF). Species were ordered by functional groups (sedge, grass, forb). No data for *Anthoxanthum* in 2016

total range of TMF (scaled) across years and snow manipulations was slightly smaller for TS than for DSM (12% and 9%). Although the difference between years was not as pronounced as for *L. helveticus*, it was statistically significant for both forbs ( $p < 0.01$ ). Highest TS were accumulated in the early melt year 2017 and lowest TS after late melt in 2016 (Table 2.2). Main flowering in *G. montanum* started at 3,200 °h (2016) to 5,500 °h (2017), in *P. aurea* at 6,300 °h (2016) to 9,900 °h (2017). For *G. montanum*, snow manipulation had a marginal influence on TS ( $p = 0.06$ ), with higher TS after snow removal (delaying effect), whereas for *P. aurea* there was no significant influence of the snow manipulations. The patterns for DSM were very similar as for TS for both species (Figure 2.3).



**Figure 2.4** TS at TMF (temperature sums at the transition to main flowering) in relation to the snowmelt date in 2016 – 2018, with census intervals, regression line (blue: no drought, orange: drought, black: no significant drought effect) and 95% CI (grey)

Overall, for the species *C. curvula*, *A. alpinum*, *H. versicolor*, and *T. alpinum* one single driver explained TMF adequately well. Relatively constant TS or DSM defined their TMF. These patterns with respect to TMF did not vary much between thresholds of 0 °C and 5 °C. The total variability in TMF was slightly larger for the 5 °C threshold (Table 2.2). In contrast, the forbs *G. montanum*, *L. helveticus*, and *P. aurea* exhibited a much larger variation in DSM and TS. For those species, photoperiod signals are likely to influence TS at TMF.

#### *Photoperiod dependent temperature sums*

To further investigate photoperiod effects, we additionally analysed the TS at TMF in relation to the date of snowmelt. For the four apparently non-photoperiod sensitive species (Table 2.3), the TS at TMF did not depend on the date of snowmelt (all  $p > 0.1$ ), evidenced by horizontal regression lines (Figure 2.4). The TS changes per one-week difference in snowmelt dates did not evoke changes that were higher than 300 °h (a typical, daily °h-value in July). Thus, the TMFs of these species were fully insensitive to photoperiod (Table 2.3). On the contrary, TS in *L. helveticus* and similarly in *G. montanum* and *P. aurea* (Table 2.3) significantly decreased with later snowmelt dates, revealing a high photoperiod sensitivity (Figure 2.4). Across our observational period, one week of difference in snowmelt dates caused TS at TMF of *L. helveticus* to decrease by 825 °h, and for the other two species, TS decreased in the range of 440 to 490 °h (Table 2.3).

**Table 2.3** The linear relation between TS at TMF (temperature sums in °h  $\geq 0$  °C) and plot-specific snowmelt dates (2016-2018). The ‘change TS per week’ indicates the change in TS per one-week later snowmelt. Test statistics are presented by log-likelihood deviances and p-values (ANOVA, n is total number of observed intervals)

Species	Change TS per week (°h / wk)	n	Log-likelihood deviance	p-value	PP sensitive
<i>C. curvula</i>	- 24	135	0.17 (1)	0.68	no
<i>A. alpinum</i> *	3	75	0.02 (1)	0.89	no
<i>H. versicolor</i>	-181	117	2.10 (1)	0.15	no
<i>G. montanum</i>	- 441	96	32.95 (1)	< 0.01	yes
<i>L. helveticus</i>	- 825	132	85.80 (1)	< 0.01	yes
<i>P. aurea</i>	- 491	111	19.16 (1)	< 0.01	yes
<i>T. alpinum</i>	20	98	0.36 (1)	0.85	no

\* Years 2017, 2018

#### **Drought effects on TMF**

Only for three out of seven species, the TMF was affected by summer drought (Table 2.2), and *A. alpinum* and *T. alpinum* both responded directly (without drought  $\times$  year interaction). Under drought, TMF of *A. alpinum* occurred five days earlier than in controls ( $p < 0.01$ ), and irrespective of the snowmelt date, drought reduced TS at TMF by 2,000 °h ( $p < 0.01$ , Figure 2.4). For *T. alpinum*, drought accelerated TMF by reducing TS by 600-700 °h compared to the controls ( $p = 0.04$ , Figure 2.4). The drought response in *P. aurea* was less uniform, accentuated by a marginally significant interaction between drought and years ( $p = 0.06$ ). Drought in 2017 reduced TS at TMF (800 °h on average) but increased it in 2018 (400 °h) in relation to controls.

**Table 2.4** ANOVA results for the flower duration (recalculated after removing non-significant variables from the full model)

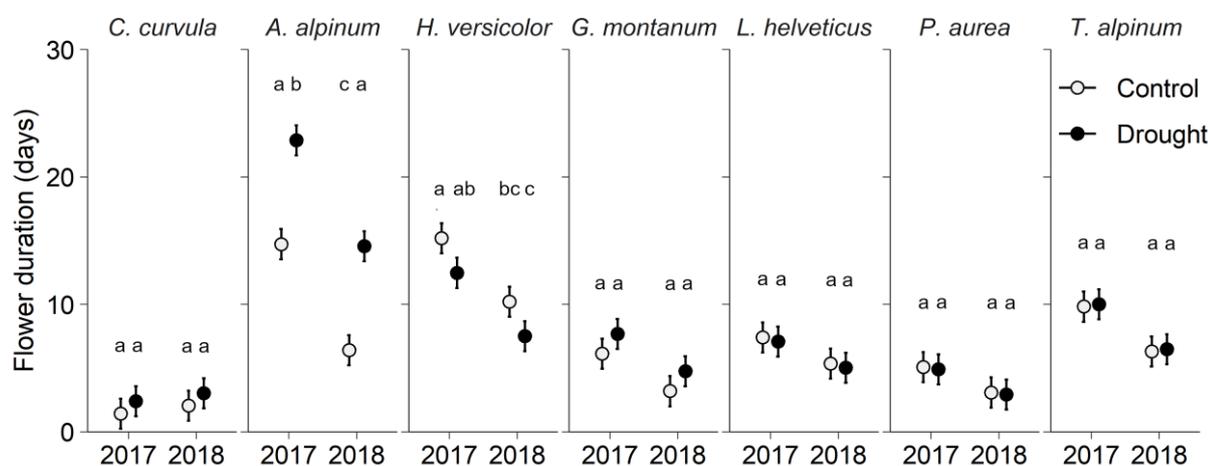
	Sum Sq	df	F value	p-value
Intercept	4638.8	1	835.5593	< 0.01
Drought	25.2	1	4.5446	0.04
Species	1346.1	6	40.4114	< 0.01
Year	229.8	1	41.3853	< 0.01
Species × Drought	206.8	6	6.2083	< 0.01
Species × Year	140.8	6	4.2281	< 0.01
Residuals	349.8	63		

### Flower duration

The flower durations in 2017 and 2018 were estimated as the time difference between TMF and the transition to flower senescence for each species and drought treatment. The flower durations in 2017, with very early melt, were longer than those in 2018 ( $p < 0.01$ , Table 2.4), and drought increased the flower duration significantly ( $p = 0.04$ ). However, the effects of both, early snowmelt and the drought treatment, were very species specific. We did not find an interaction effect between drought and years ( $p = 0.61$ ).

For individual species, only the two grasses *A. alpinum* and *H. versicolor* strongly differed in flower durations between the two years. *A. alpinum* flowered 15 days in the early snowmelt year 2017 and 6 days in 2018. Similarly, *H. versicolor*'s flower duration in 2017 lasted 15 days and 10 days in 2018, respectively ( $p < 0.01$ ). In the forb *T. alpinum*, the flower duration was marginally longer in 2017 than in 2018, (10 days in 2017 and 6 days in 2018;  $p = 0.06$ ). For the species with a short flower duration (*C. curvula*, *G. montanum*, *L. helveticus* and *P. aurea*) in the range of one to five days, no significant differences between the two years were observed.

Only one species, *A. alpinum*, flowered significantly longer under drought (8 days in both years;  $p < 0.01$ , Figure 2.5). As mentioned above, our results suggest slightly longer flower durations for all species in 2017 than in 2018, except for *C. curvula*. In 2017, the



**Figure 2.5** Flowering duration (mean  $\pm$  se) for the seven plant species in 2017 and 2018 ( $n = 3$ , without snow manipulations). Open symbols: controls, filled symbols: drought (moderate and intense averaged). Letters refer to Tukey post-hoc comparisons by species

mean July air temperatures at the site were 1.0 K lower than in 2018 (Figure S2.2 for on-site weather conditions).

## Discussion

This snow manipulation and summer precipitation exclusion experiment at 2,500 m a.s.l., revealed that the flowering phenology of the main species in this alpine grassland closely pursue snowmelt date and the microclimatic conditions thereafter. Drought had a minor influence on TMF, most likely because flowering started before the soil had gone through the most severe dehydration. DOY / PP at snowmelt varied by 38 days among the three different years (2016-2018) and the snow manipulations. We were able to distinguish between non-photoperiod sensitive species (*C. curvula*, *A. alpinum*, *H. versicolor*, *T. alpinum*) and species that closely track the photoperiod (*L. helveticus*, *G. montanum*, *P. aurea*). In species exhibiting photoperiodism, later snowmelt accelerated TMF and caused a higher degree of flowering synchrony. This increased synchrony may be of larger importance for plant species that depend on pollinators, as all three photoperiod sensitive species are insect-pollinated forbs. The non-photoperiod sensitive species (all but one wind pollinated) showed very similar TS at TMF across experimental manipulations and years.

### The role of snowmelt and microclimate

The number of days elapsed since snowmelt (DSM) at TMF was consistently less variable than DOY at TMF, even for photoperiod sensitive species. Snow removal led to earlier flowering irrespective of DOY and snow addition caused later flowering. This confirms other snow manipulation studies performed in (sub-)alpine and arctic ecosystems (e.g., Totland and Alatalo 2002; Lambert *et al.* 2010; Wipf and Rixen 2010). Particularly for *C. curvula*, TS at the TMF varied by 45% less than DSM. Hence, in these species TMF was determined by the snowmelt date, but with a time lapse defined by species-specific heat sum requirements. Low temperatures immediately after snowmelt may delay the floral development. The later snowmelt occurs, the stronger the correlation of TS and DSM. For late flowering species (e.g., *H. versicolor*), DSM and TS may thus be substituted by each other as drivers.

We assume that the highly opportunistic flowering behaviour of the dominant species *C. curvula* that was also observed by Wagner and Reichegger (1997), is related to a rather complete preformation of the inflorescences (Erschbamer *et al.* 1994), allowing such rapid flowering. The less complete inflorescences are preformed, the greater the influence of weather conditions after snowmelt on TMF. In some species, preformation (primary induction *sensu* Heide, 1990) may take up to two years prior to flowering (Diggle and Mulder 2019). The tight coupling of flowering with snowmelt (with only minor weather-dependent delay) in the wind pollinated *C. curvula* creates topography driven reproduction cohorts which flower simultaneously - tracking the distinct small-scale snowmelt patterns. This may promote ecotype formation (reproductive guilds) over longer time periods. TMF in *T. alpinum* also correlated with TS. This species forms very large and complex inflorescences, the full development of which requires more time, and thus, depends more strongly on the weather conditions in the weeks after snowmelt.

Covering a wide range of high-latitude and high-elevation phenological observations, Prév y *et al.* (2019) demonstrated that under current global warming, late flowering species may start flowering earlier in the season. In contrast to our results, Pr v y and co-authors assumed that early

flowering species followed photoperiod more closely (in addition to snowmelt date), and late flowering species pursued the temperature regime. In contrast, Wadgyamar *et al.* (2018) observed that in six subalpine forb species, flowering advanced fastest in earlier flowering species. Our data show that both, an early flowering species *C. curvula* as well as a later flowering species *T. alpinum* were triggered by thermal sums. Both species required higher TS till TMF after snow removal, but lower TS following snow addition, suggesting a slight flowering synchronization in these two non-photoperiod sensitive species.

Whether an earlier start of the seasonal phenological development will also yield reproductive benefits is rather questionable (Gugger *et al.* 2015). A potential trade-off of an earlier snowmelt date is the greater risk of late freezing events (Wipf *et al.* 2009). In a 31-yr-long phenology study in the Rocky Mountains, Inouye (2008) found a higher degree of frost damage after early snowmelt. Number of flowers, leaf growth and survival of the evergreen forb *Gentiana nipponica* were significantly reduced in populations with one-month earlier snowmelt (Kawai and Kudo 2018). However, occasional frost damages do not necessarily cause a population decline, given that these taxa are all long lived and, to variable degree, clonal. Observations in the subalpine sunflower *Helianthella quinquenervis* revealed that early snowmelt (between 1999 and 2012) increased the risk of frost damages, but it also enhanced the number of flowers in the following growing season (Iler *et al.* 2019). The authors suggested a higher allocation of assimilates to preforming buds for the next year, thus, overcompensating for the frost damages.

### The role of photoperiod

The fact that TMF in three of the seven species was modulated by photoperiod underlines the observations by Keller and Körner (2003) that half of 23 alpine and nival species revealed a photoperiod effect on flowering (though much stronger than observed here). Hence, these three species were unable to utilize an earlier onset of the snowfree period. The photoperiod control became less decisive once a minimum daylength requirement had been surpassed. Yet, the plants studied by Keller and Körner (2003) started the growing season in daylight growth chambers with a 4 h shorter photoperiod than would normally occur in the field. At our field site, such a difference would correspond to a snowmelt in mid-March and even the exceptionally early snowmelt in 2017 (3.5 weeks earlier) corresponds to a photoperiod difference in the range of minutes only (maximum of 10 min). At field conditions, it is therefore unlikely that differences in photoperiod of several hours will come into action in a warmer future. Iler *et al.* (2013) studied 58 subalpine plant species over 38 years and found that peak flowering linearly advanced with snowmelt dates in 38% of all species. However, roughly one fifth of the species had longer development times when snowmelt occurred before a certain date. By using a similar time-to-event analysis as in our study, with temperature sums (soil temperature), snowmelt dates and photoperiod, Hülber *et al.* (2010) concluded that temperature was the dominant driver for the transition to flowering in all ten alpine species tested along a natural snowmelt gradient.

The challenge with such conclusions is that these three components, the date of snowmelt, the temperature conditions and photoperiod interact in a non-linear way on species that differ in their degree of flower bud preformation (and thus, the time required to grow an inflorescence). When conditions are favourable and plants enter the winter with almost completed flower buds, it seems that temperature after snowmelt is the only factor driving TMF. The role of photoperiod comes into action as a modulating factor when snowmelt occurs much earlier (as was observed in 2017). This gradual nature of the photoperiod influence complicates the interpretation. When species are released at a date at which they are sensitive to photoperiod, they seem to require more thermal

energy (TS) after earlier snowmelt till flowering. We found such a gradual influence in *L. helveticus* and less pronounced in *G. montanum* and *P. aurea*. For the observed period, TS at TMF increased linearly with earlier snowmelt dates, including a year with 3.5-wk earlier snowmelt than usual.

For snowbed species, reduced heat requirements for flowering have been observed after late snowmelt (Carbognani *et al.* 2016). Larl and Wagner (2006) noticed a substantially faster seasonal cycle of *Saxifraga oppositifolia* in subnival (2.5 months) than in alpine populations (4-month season), along with lower temperature sums for reaching all developmental stages. They hypothesized that the evolved genotypes at the subnival sites require less thermal energy. This is in line with results of Prock and Körner (1996), who unveiled an origin-specific influence of photoperiod on flowering and plant senescence (but not for the *Rosaceae* species they included) by means of a cross-continental transplant experiment. The modulating effect of photoperiod on phenology may enhance such micro-evolutionary processes.

### Drought effects

TMF was largely unaffected by summer drought. Only the grass *A. alpinum* showed a pronounced shift by a five-day earlier flowering and a longer flower duration under drought (plus eight days). A similar response was observed in a lowland grassland, where flowering under drought lasted four days longer (Jentsch *et al.* 2009). The TMF of *C. curvula*, *H. versicolor*, *G. montanum*, and *L. helveticus* remained completely unaffected by drought, similar to findings for the Bavarian Alps by Cornelius *et al.* (2013). These authors explored drought effects along an elevational gradient (800–2,000 m a.s.l.) and in contrast to the lower elevation sites, plants at higher elevations did not respond to drought. However, the drought treatment in the study of Cornelius and co-authors started late (four weeks after snowmelt, thus missing the most critical period). The transitions to flowering of 20 montane and alpine species was clearly advanced by an elevational down-shift of 1000 m asl, but not by drought alone, revealed by a transplant experiment (Gugger *et al.* 2015). Sheltering off rain did also not affect flowering phenology in a montane grassland in the French Massif Central (Bloor *et al.* 2010). In these cases, it is very likely that rain exclusion did not evoke substantial responses in flowering phenology because flowering occurred early in the season when the soil profile still contained sufficient moisture, causing soil profile depth to become an important co-variable. However, our IR surface temperatures point to prevalent stomatal closures under drought, underpinning that our alpine plants experienced water shortage *in situ*.

### Flower duration

The longer flower duration observed in the early melt year 2017 compared to 2018 could compensate for the cooler early season weather and presumably, less abundant pollinators. Several studies in montane grassland have noted prolonged flower durations in case of early snowmelt (e.g., Dunne *et al.* 2003; Pardee *et al.* 2019). Alpine forbs have been shown to be very plastic in their flower durations in the absence of pollinators and/or under bad weather conditions (Trunschke 2017; see the review in Körner 2021). Extended flowering may facilitate higher visitation numbers by insects (Pardee *et al.* 2019). And in case of a specific plant-pollinator dependency, flowering time can be decoupled from pollinator activity, as was suggested for the ephemeral *Corydalis ambigua* and its bumblebee under early snowmelt (Kudo and Cooper 2019). However, alpine plants commonly receive a very broad pollinator spectrum (e.g., Erhardt 1993; Tiusanen *et al.* 2019) and often have several cohorts of flowers, making pollinator limitation for

reproduction very unlikely (Wagner *et al.* 2016; Arroyo *et al.* 2017), in addition to the fact that many alpine plants grow clonally (Körner 2021).

## Conclusions

Our snowmelt manipulation and the natural variation of snowmelt date demonstrated the importance of snowmelt date and the subsequent microclimatic conditions for flowering phenology in late successional alpine grassland, with photoperiod playing a species-specific modulating role in at least three of the seven species studied. A 3.5-weeks earlier snowmelt in the exceptional year 2017 reinforced the photoperiod effect. Even subtle changes in the snowmelt regime modified the heat sum required till flowering, suggesting a complex interaction between temperature and photoperiod. We therefore warn against simplistic projections of correlations between climatic warming (commonly extrapolated from weather stations), snowmelt date and flowering phenology. The earlier snow melts, the stronger become photoperiod constraints, responses, presumably selected for escaping freezing damage. These evolutionary constraints to phenology will limit potential benefits in terms of growth and reproduction of current alpine grassland taxa and their currently abundant ecotypes by a longer alpine season in a warmer climate.

## References

- Arroyo MTK, Pacheco DA, Dudley LS (2017) Functional role of long-lived flowers in preventing pollen limitation in a high elevation outcrossing species. *AoB Plants* 9:1–12. doi: 10.1093/aobpla/plx050
- Bloor JMG, Pichon P, Falcimagne R, Leadley P, Soussana J-F (2010) Effects of warming, summer drought, and CO<sub>2</sub> enrichment on aboveground biomass production, flowering phenology, and community structure in an upland grassland ecosystem. *Ecosystems* 13:888–900. doi: 10.1007/s10021-010-9363-0
- Canaday BB, Fonda RW (1974) The influence of subalpine snowbanks on vegetation pattern, production, and phenology. *Bull Torrey Bot Club* 101:340–350
- Carbognani M, Bernareggi G, Perucco F, Tomaselli M, Petraglia A (2016) Micro-climatic controls and warming effects on flowering time in alpine snowbeds. *Oecologia* 182:573–585. doi: 10.1007/s00442-016-3669-3
- Cornelius C, Leingärtner A, Hoiss B, Menzel A (2013) Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. *J Exp Bot* 64:241–251. doi: 10.1093/jxb/err313
- de Boeck HJ, Bassin S, Verlinden M, Zeiter M, Hiltbrunner E (2016) Simulated heat waves affected alpine grassland only in combination with drought. *New Phytol* 209:531–541. doi: 10.1111/nph.13601
- Dietrich L, Körner C (2014) Thermal imaging reveals massive heat accumulation in flowers across a broad spectrum of alpine taxa. *Alp Bot* 124:27–35. doi: 10.1007/s00035-014-0123-1
- Diggle PK, Mulder CPH (2019) Diverse developmental responses to warming temperatures underlie changes in flowering phenologies. *Integr Comp Biol* 59:559–570. doi: 10.1093/icb/icz076
- Dunne JA, Harte J, Taylor KJ (2003) Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. *Ecol Monogr* 73:69–86. doi: 10.1890/0012-9615(2003)073

- Erhardt A (1993) Pollination of the edelweiss, *Leontopodium alpinum*. *Bot J Linn Soc* 111:229–240. doi: <https://doi.org/10.1111/j.1095-8339.1993.tb01900.x>
- Erschbamer B, Winkler J, Wagner J (1994) The vegetative and generative development of three *Carex curvula* in the Central Alps. *Flora* 189:277–286
- Gugger S, Kesselring H, Stöcklin J, Hamann E (2015) Lower plasticity exhibited by high- versus mid-elevation species in their phenological responses to manipulated temperature and drought. *Ann Bot* 116:953–962. doi: 10.1093/aob/mcv155
- Heide OM (2001) Photoperiodic control of dormancy in *Sedum telephium* and some other herbaceous perennial plants. *Physiol Plant* 113:332–337. doi: 10.1034/j.1399-3054.2001.1130305.x
- Heide OM (1985) Physiological aspects of climatic adaptation in plants with special reference to high-latitude environments. *Plant Prod north Proc from plant Adapt Work Tromso, Norway, September 4-9, 1983* 1–22
- Heide OM (1990) Dual floral induction requirements in *Phleum alpinum*. *Ann Bot* 66:687–694. doi: 10.1093/oxfordjournals.aob.a088083
- Heide OM (1992) Flowering strategies of the high-arctic and high-alpine snow bed grass species *Phippsia algida*. *Physiol Plant* 85:606–610. doi: 10.1111/j.1399-3054.1992.tb04761.x
- Heide OM (2005) Ecotypic variation among European arctic and alpine populations of *Oxyria digyna*. *Arctic, Antarct Alp Res* 37:233–238. doi: 10.1657/1523-0430(2005)037[0233:EVAEAA]2.0.CO;2
- Heide OM, Pedersen K, Dahl E (1990) Environmental control of flowering and morphology in the high-arctic *Cerastium regelii*, and the taxonomic status of *C. jenisejense*. *Nord J Bot* 10:141–147. doi: 10.1111/j.1756-1051.1990.tb01761.x
- Hock R, Rasul G, Adler C, Cáceres B, Gruber S, Hirabayashi Y, Jachson M, Käab A, Kang S, Kutuzov S, Milner A, Molau U, Morin S, Orlove B, Steltzer H (2019) High mountain areas. In: H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama NMW (ed) IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. World Meteorological Organization, in press. p 202, p 32
- Hülber K, Winkler M, Grabherr G (2010) Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. *Funct Ecol* 24:245–252. doi: 10.1111/j.1365-2435.2009.01645.x
- Iler AM, Compagnoni A, Inouye DW, Williams JL, Anderson A, Miller TEX, CaraDonna PJ (2019) Reproductive losses due to climate change - induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *J Ecol* 107:1931–1943. doi: 10.1111/1365-2745.13146
- Iler AM, Høye TT, Inouye DW, Schmidt NM (2013) Nonlinear flowering responses to climate: Are species approaching their limits of phenological change? *Philos Trans R Soc B Biol Sci* 368:13–16. doi: 10.1098/rstb.2012.0489
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362. doi: 10.1890/06-2128.1
- IPCC (2018) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner H, et al. (eds) *Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change*. Geneva,

- Switzerland, pp 374–381
- Jentsch A, Kreyling J, Boettcher-Treschkow J, Beierkuhnlein C (2009) Beyond gradual warming: Extreme weather events alter flower phenology of European grassland and heath species. *Glob Chang Biol* 15:837–849. doi: 10.1111/j.1365-2486.2008.01690.x
- Kawai Y, Kudo G (2018) Variations in ramet performance and the dynamics of an alpine evergreen herb, *Gentiana nipponica*, in different snowmelt conditions. *Am J Bot* 105:1813–1823. doi: 10.1002/ajb2.1186
- Keller F, Ephane ST, Beniston M (2005) Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in alpine terrain. *Clim Change* 72:299–319. doi: 10.1007/s10584-005-5360-2
- Keller F, Körner C (2003) The role of photoperiodism in alpine plant development. *Arctic, Antarct Alp Res* 35:361–368. doi: 10.1657/1523-0430(2003)035[0361:TROPIA]2.0.CO;2
- Klein G, Vitasse Y, Rixen C, Marty C, Rebetez M (2016) Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than later snow onset. *Clim Change* 139:637–649. doi: 10.1007/s10584-016-1806-y
- Klein JP, Moeschberger ML (2003) Survival analysis. Techniques fo censored and truncated data, 2nd edn. Springer, New York, p 535
- Körner C (2021) Alpine plant life. Functional plant ecology of high mountain ecosystems, 3rd edn. Springer, Cham. p 496
- Körner C, Hiltbrunner E (2018) The 90 ways to describe plant temperature. *Perspect Plant Ecol Evol Syst* 30:16–21. doi: 10.1016/j.ppees.2017.04.004
- Kudernatsch T, Fischer A, Bernhardt-Römermann M, Abs C (2008) Short-term effects of temperature enhancement on growth and reproduction of alpine grassland species. *Basic Appl Ecol* 9:263–274. doi: 10.1016/j.baae.2007.02.005
- Kudo G, Cooper EJ (2019) When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. *Proc R Soc - Biol Sci* 286:20190573
- Lambert AM, Miller-Rushing AJ, Inouye DW (2010) Changes in snowmelt date and summer precipitation affect the flowering phenology of *Erythronium grandiflorum* (glacer lily; Liliaceae). *Am J Bot* 97:1431–1437. doi: 10.3732/ajb.1000095
- Larl I, Wagner J (2006) Timing of reproductive and vegetative development in *Saxifraga oppositifolia* in an alpine and a subnival climate. *Plant Biol* 8:155–166. doi: 10.1055/s-2005-872888
- Lauber K, Wagner G, Gyax A (2018) *Flora helvetica*, 6th edn. Haupt Verlag, Bern. p 1686
- Lenth R, Henrik S, Love J, Buerkner P, Herve M (2019) R package emmeans: Estimated marginal means, aka least-squares means. p 81
- Leuschner C, Ellenberg H (2017) Ecology of central European non-forest vegetation: coastal to alpine, natural to man-made habitats. *Vegetation ecology of central Europe, Volume II, extended v.* Springer, Cham. p. 1094
- Livensperger C, Steltzer H, Darrouzet-Nardi A, Sullivan PF, Wallenstein M, Weintraub MN (2016) Earlier snowmelt and warming lead to earlier but not necessarily more plant growth. *AoB Plants* 8:plw021. doi: 10.1093/aobpla/plw021
- Marty C (2008) Regime shift of snow days in Switzerland. *Geophys Res Lett* 35:L12501. doi: 10.1029/2008GL033998
- Meloche CG, Diggle PK (2001) Preformation, architectural complexity, and developmental flexibility in *Acomastylis rossii* (Rosaceae). *Am J Bot* 88:980–991. doi: 10.2307/2657079

- Molau U, Nordenhäll U, Eriksen B (2005) Onset of flowering and climate variability in an alpine landscape: A 10-year study from Swedish Lapland. *Am J Bot* 92:422–431. doi: 10.3732/ajb.92.3.422
- Oberdorfer E (2001) *Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete*, 8th edn. Ulmer, Germany, p 1051
- Pardee GL, Jensen IO, Inouye DW, Irwin RE (2019) The individual and combined effects of snowmelt timing and frost exposure on the reproductive success of montane forbs. *J Ecol* 107:1970–1981. doi: 10.1111/1365-2745.13152
- Prevéy JS, Rixen C, Rüger N, Høye TT, Bjorkman AD, Myers-smith IH, Elmendorf SC, Ashton IW, Cannone N, Chisholm CL, Clark K, Cooper EJ, Elberling B, Fosaa AM, Henry GHR, Hollister RD, Jónsdóttir IS, Klanderud K, Kopp CW, Lévesque E, Mauritz M, Molau U, Natali SM, Schuur E, Semenchuk PR, Smith JG, Suding KN, Totland Ø, Troxler T, Venn S, Wahren C-H, Welker JM, Wipf S (2019) Warming shortens flowering seasons of tundra plant communities. *Nat Ecol Evol* 3:45–52. doi: 10.1038/s41559-018-0745-6
- Prock S, Körner C (1996) A cross-continental comparison of phenology, leaf dynamics and dry matter allocation in Arctic and temperate zone herbaceous plants from contrasting altitudes. *Ecol Bull* 45:93–103
- R Core Team (2019) R: A language and environment for statistical computing
- Ram J, Singh SP, Singh JS (1988) Community level phenology of grassland above treeline in Central Himalaya, India. *Arct Alp Res* 20:325–332
- Rosbakh S, Leingärtner A, Hoiss B, Krauss J, Steffan-dewenter I, Poschlod P (2017) Contrasting effects of extreme drought and snowmelt patterns on mountain plants along an elevation gradient. *Front Plant Sci* 8:1–17. doi: 10.3389/fpls.2017.01478
- Schäppi B, Körner C (1996) Growth responses of an alpine grassland to elevated CO<sub>2</sub>. *Oecologia* 105:43–52
- Scherrer D, Körner C (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Glob Chang Biol* 16:2602–2613. doi: 10.1111/j.1365-2486.2009.02122.x
- Scherrer SC, Wüthrich C, Croci-Maspoli M, Weingartner R, Appenzeller C (2013) Snow variability in the Swiss Alps 1864–2009. *Int J Climatol* 33:3162–3173. doi: 10.1002/joc.3653
- Schmid S, Hiltbrunner E, Spehn E, Lüscher A, Scherer-Lorenzen M (2011) Impact of experimentally induced summer drought on biomass production in alpine grassland. *Grassl Sci Eur* 16:214–216
- Steger C, Kotlarski S, Jonas T, Schär C (2013) Alpine snow cover in a changing climate: A regional climate model perspective. *Clim Dyn* 41:735–754. doi: 10.1007/s00382-012-1545-3
- Therneau TM (2015) A Package for Survival Analysis in S
- Tiusanen M, Huotari T, Hebert PDN, Andersson T, Asmus A, Bêty J, Davis E, Gale J, Hardwick B, Hik D, Körner C, Lanctot RB, Loonen MJJE, Partanen R, Reischke K, Saalfeld ST, Senez-Gagnon F, Smith PA, Šulavík J, Syvänperä I, Urbanowicz C, Williams S, Woodard P, Zaika Y, Roslin T (2019) Flower-visitor communities of an arcto-alpine plant—Global patterns in species richness, phylogenetic diversity and ecological functioning. *Mol Ecol* 28:318–335. doi: 10.1111/mec.14932
- Totland O, Alatalo JM (2002) Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the Arctic / Alpine herb, *Ranunculus glacialis*. *Oecologia* 133:168–175
- Trunschke J (2017) Plasticity of flower longevity in alpine plants is increased in populations from

high elevation compared to low elevation populations. *Alp Bot* 127:41–51. doi: 10.1007/s00035-016-0176-4

Wadgyamar SM, Ogilvie JE, Inouye DW, Weis AE, Anderson JT (2018) Phenological responses to multiple environmental drivers under climate change: insights from a long-term observational study and a manipulative field experiment. *New Phytol* 218:517–529. doi: 10.1111/nph.15029

Wagner J, Lechleitner M, Hosp D (2016) Pollen limitation is not the rule in nival plants: A study from the European Central Alps. *Am J Bot* 103:375–387. doi: 10.3732/ajb.1500214

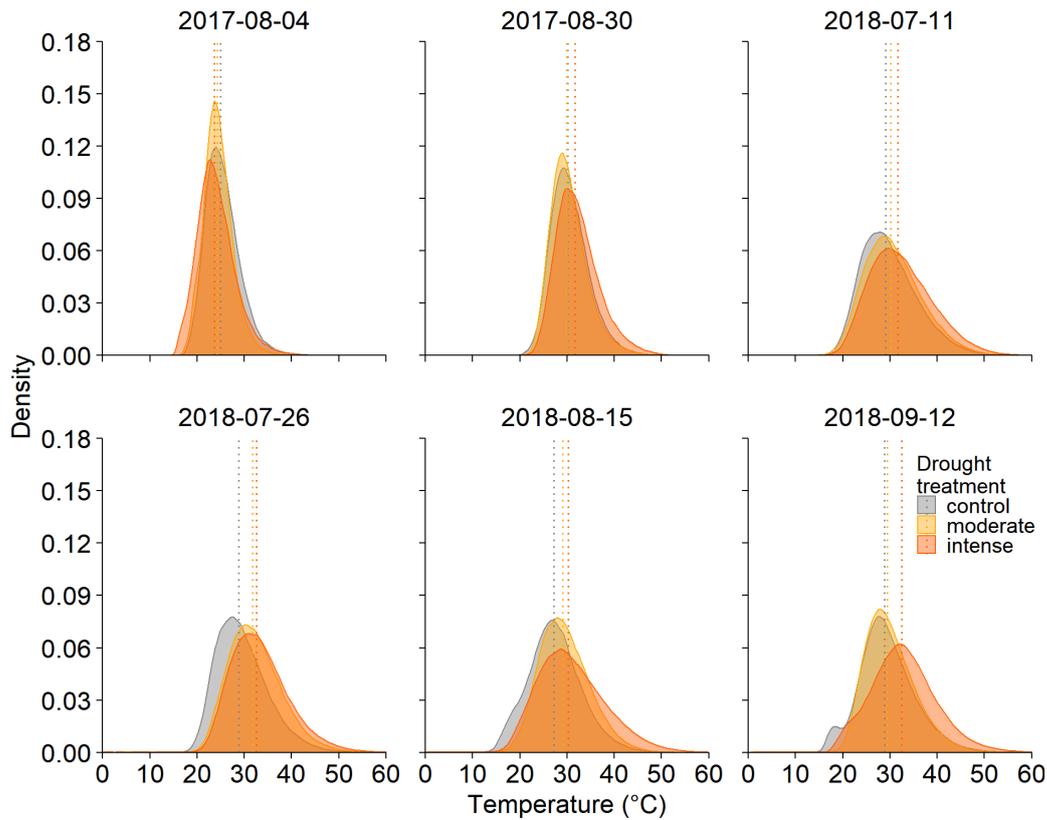
Wagner J, Reichegger B (1997) Phenology and seed development of the alpine sedges *Carex curvula* and *Carex firma* in response to contrasting topoclimates. *Arct Alp Res* 29:291–299

Weingartner R, Viviroli D, Schädler B (2007) Water resources in mountain regions: a methodological highland-lowland-system. *Hydrol Process* 21:578–585. doi: 10.1002/hyp

Wipf S, Rixen C (2010) A review of snow manipulation experiments in arctic and alpine tundra ecosystems. *Polar Res* 29:95–109. doi: 10.1111/j.1751-8369.2010.00153.x

Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Clim Change* 94:105–121. doi: 10.1007/s10584-009-9546-x

## Supplemental material for chapter 2



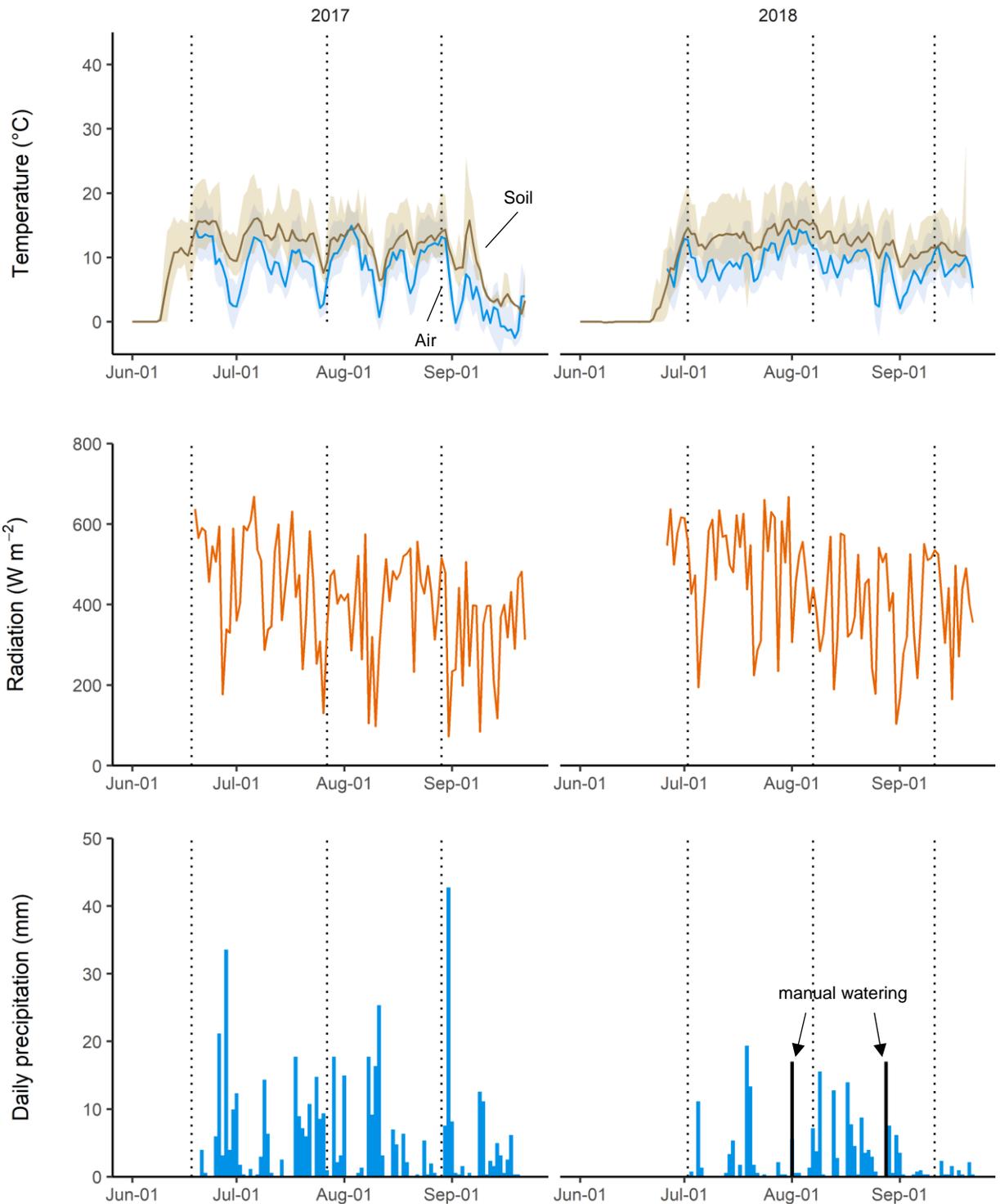
**Figure S2.1** Density plots of the surface temperature of the central 1x1 m plot during six different dates, recorded with an IR thermal camera (15 plots per drought treatment). Dotted lines indicate the median temperature. The moderate drought treatment lasted until Jul 28<sup>th</sup> in 2017 and Aug 7<sup>th</sup> in 2018

**Table S2.1** Surface temperatures of the central 1x1 m plot (median temperature derived for each single plot, listed as mean  $\pm$  sd for each drought treatment) for two dates in 2017 and for four dates in 2018, measured with an IR thermal camera. Letters refer to the Tukey post-hoc comparisons of the median surface temperature (n = 15)

Date	Drought treatment	Surface temperature (°C)
2017-08-04	control	24.7 $\pm$ 2.2 <sup>a</sup>
	moderate	24.1 $\pm$ 2.7 <sup>a</sup>
	intense	23.6 $\pm$ 2.4 <sup>a</sup>
2017-08-30	control	30.2 $\pm$ 1.2 <sup>a</sup>
	moderate	30.0 $\pm$ 1.4 <sup>ab</sup>
	intense	31.2 $\pm$ 1.1 <sup>b</sup>
2018-07-11	control	29.1 $\pm$ 2.4 <sup>a</sup>
	moderate	30.1 $\pm$ 2.4 <sup>ab</sup>
	intense	31.5 $\pm$ 2.7 <sup>b</sup>
2018-07-26	control	28.7 $\pm$ 2.5 <sup>a</sup>
	moderate	31.7 $\pm$ 2.2 <sup>b</sup>
	intense	32.4 $\pm$ 1.7 <sup>b</sup>
2018-08-15	control	26.7 $\pm$ 3.7 <sup>a</sup>
	moderate	29.0 $\pm$ 2.3 <sup>ab</sup>
	intense	30.6 $\pm$ 4.2 <sup>b</sup>
2018-09-12	control	29.0 $\pm$ 4.4 <sup>a</sup>
	moderate	29.7 $\pm$ 3.4 <sup>a</sup>
	intense	32.5 $\pm$ 5.1 <sup>b</sup>

**Table S2.2** Thermal sums  $TS \geq 5^\circ\text{C}$  ( $^\circ\text{h}$ ) accumulated at TMF (2016-2018). Left: values for the TMF following snow removal (rem.), snow addition (add.) and drought are shown as difference to the control. The difference of the drought treatment to the control is averaged over snow treatments. Right: test statistics for explaining variables for TMF (Abbreviations D: drought treatment Y: year)

Species	Driver	Y	Onset control	Difference to control			Expl. Var	LR $X^2$ (df)	p-value	Expl. Var	LR $X^2$ (df)	p-value
				rem.	add.	D						
<i>C. curvula</i>	$TS \geq 5^\circ\text{C}$ ( $^\circ\text{h}$ )	2016	1650	250	-50		S	6.00 (2)	<b>0.05</b>	D	2.18 (1)	0.14
		2017	1500	300	-100	300	Y	12.34 (2)	<b>&lt;0.01</b>	D×S	3.26 (2)	0.20
		2018	1150	150	150	150	S×Y	1.66 (4)	0.80	D×Y	0.45 (1)	0.50
<i>G. montanum</i>	$TS \geq 5^\circ\text{C}$ ( $^\circ\text{h}$ )	2016	1800	650	150		S	3.99 (2)	0.14	D	1.54 (1)	0.22
		2017	3350	0	-100	-50	Y	68.53 (2)	<b>&lt;0.01</b>	D×S	1.15 (2)	0.56
		2018	2950	200	0	-300	S×Y	3.59 (4)	0.46	D×Y	0.69 (1)	0.40
<i>P. aurea</i>	$TS \geq 5^\circ\text{C}$ ( $^\circ\text{h}$ )	2016	3650	250	850		S	0.42 (2)	0.81	D	1.28 (1)	0.26
		2017	6100	-750	-400	650	Y	27.58 (2)	<b>&lt;0.01</b>	D×S	0.15 (2)	0.93
		2018	5850	150	-150	-150	S×Y	5.99 (4)	0.20	D×Y	3.20 (1)	0.07
<i>T. alpinum</i>	$TS \geq 5^\circ\text{C}$ ( $^\circ\text{h}$ )	2016	5950	1050	-100		S	13.81 (2)	<b>&lt;0.01</b>	D	2.47 (1)	0.12
		2017	6100	-450	150	-500	Y	2.40 (2)	0.3	D×S	0.09 (2)	0.96
		2018	5750	-300	700	-350	S×Y	2.89 (4)	0.58	D×Y	0.06 (1)	0.81



**Figure S2.2** Weather conditions at the study site in 2017 and 2018. Upper graph: mean daily air temperatures with minimum and maximum and mean daily soil temperature (3-4cm depth) of a control plot. Middle graph: daily radiation means, with threshold of  $20 W m^{-2}$ . Lower graph: daily precipitation with watering of controls in 2018 ( $2 \times 17 L$ ). Note that the weather measurements started earlier in 2017 than 2018. Dotted lines indicate the start of the drought treatment, and the end of the moderate and intense drought treatment, respectively





## Chapter 3 - Summer drought reduces aboveground biomass formation in alpine grassland but does not constrain nitrogen uptake of *Carex curvula*

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### Keywords

Snowmelt date, summer drought, alpine, late successional grassland, biogeochemical cycles

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## Abstract

Rising temperatures and shifting precipitation patterns due to climate change may extend growing seasons but with a higher risk of summer drought. To delineate the combined effects of these two major climatic changes on the biomass production and nutrient cycles of a late successional alpine grassland, we set up a snow manipulation experiment, combined with summer drought through 5-wk and 10.5-wk rain exclusion. In addition to snow addition and removal for manually shifting the snowmelt dates, the experimental years 2016-2018 included an exceptionally early start of the growing season in 2017.

Experimentally prolonging the growing season neither enhanced the overall, nor the above- or below-ground biomass production. Five weeks of rain exclusion did not significantly affect the above-ground biomass, but increased the overall root production by 19%. After rain exclusion during almost the entire growing season (10.5 weeks), the total above-ground biomass production declined by 19%, whereas the root production was similar as on controls.

The response of the above-ground biomass production differed between functional groups: 5-wk of drought led to increased biomass production in the dominant sedge *Carex curvula* only, whereas the 10.5-wk drought caused a decline by 17%, and even by 25% in forbs.

The decomposition of on-site litter mainly took place under the insulating snow. Thus, subsequent snowmelt dates and summer drought had no measurable effect on the mass loss of litter bags. Additional burying of maize litter enriched in  $^{15}\text{N}$  (stable nitrogen isotope; 370 ‰) revealed that the nitrogen released over the winter months was already assimilated in the foliar tissue in the first weeks after the growing season. The subsequent nitrogen uptake was not diminished by summer drought. Although not statistically significant, we found a weak trend towards hindered root foraging under drought. An additional nutrient layer at 5 cm soil depth increased the root production by 77.7% on controls, but only by 12.9% after five weeks of drought. We conclude that late successional alpine grasslands are surprisingly robust against shifting snowmelt dates and summer drought. However, droughts will evoke contrasting responses in the above- and the below-ground biomass formation, and thus, future research should increasingly focus on the below-ground processes of alpine ecosystems under drought.

## Introduction

Alpine regions are particularly affected by global warming because air temperatures have risen faster in the Alps than in the lowlands (Rebetez and Reinhard 2008; Ceppi et al. 2012; NCCS 2018a; Hock et al. 2019). Rising temperatures and the resulting earlier snowmelt could prolong the growing season of alpine plants considerably (Chapter 1). Extended growing seasons may coincide with more frequent and more severe summer droughts (Calanca 2007; Rajczak et al. 2013; Gobiet et al. 2014; IPCC 2018). For the alpine and subalpine region, plant responses to both early snowmelt and summer drought have mostly been studied separately (but see Cornelius et al. 2013). However, to assess the future ecosystem functioning of alpine regions hosting exceptional biodiversity (Körner 2003) and sustaining our water balance (Hock et al. 2019), it is crucial to explore the combined effect of early snowmelt and of summer drought.

Although up to one half of the alpine species may be sensitive to photoperiod (Keller and Körner 2003, Chapter 2), there is evidence that earlier snowmelt and rising temperatures cause an advancement in the phenology of many alpine and montane plant species (e.g., Hülber et al. 2006; Wipf et al. 2009, and see Chapter 2). But earlier plant development does not necessarily lead to enhanced biomass formation, as an increased risk for freezing damages after earlier melt may impair plant growth (e.g., Inouye 2008; Wipf et al. 2009).

An experimentally induced summer drought in an alpine grassland for six and twelve weeks reduced the above-ground biomass by 12-35% (Schmid et al. 2011), but it increased the below-ground biomass by 47-50% (Schmid 2017). Above-ground responses to drought have been studied more thoroughly than the below-ground root production. Blume-Werry et al. (2017) documented that a nine-day earlier snowmelt in a high-latitude heath and a meadow advanced the growth of above-ground shoots, but not of fine roots. One can therefore not conclude from the easily observable above-ground phenology and growth to the below-ground plant development. Under drought, plant biomass allocation may preferentially shift from above-ground to below-ground organs. Hence, concordant with the *sensu* functional growth analysis (Körner 2014), the total plant biomass production as well as its allocation to the different plant compartments has to be considered.

The productivity of high-elevation and high-latitude ecosystem is often regarded to be limited or strongly influenced by nutrient availability (Jonasson et al. 1999; Körner 2003). The ongoing climatic changes may affect biogeochemical processes of alpine ecosystems, including the nutrient cycles of alpine ecosystems (Gavazov 2010). The majority of alpine plants perform a pronounced resorption and recycling of nutrients (Körner 2003). During leaf senescence, *Carex curvula* resorbs roughly two thirds of its nitrogen content from the leaves (Schäppi and Körner 1997). For eleven subarctic plant species it was further shown that nutrients are also resorbed from senescing fine roots, with a resorption rate of 27% for nitrogen (N) and 57% for phosphorus (Freschet et al. 2010). Despite the high recycling, alpine plants depend on additional nutrient inputs. The main input comes through mineralisation of organic material, mainly litter (root, leaf litter) to inorganic compounds. As the decomposition of litter is slower in alpine ecosystems than in the lowland, a reduced decomposition may limit the plant productivity and has implications for the species distribution in the longer term (Seastedt et al. 2001). However, many alpine plants are capable to take up larger, organic N compounds (Lipson and Näsholm 2001; Miller and Bowman 2003). Increased atmospheric N deposition, particularly N deposited through rain and snow acts a further N source for alpine plants (Hiltbrunner et al. 2005; Kosonen et al. 2019). Alpine species,

especially *Carex* species, seem to readily respond to this additional source and may out-compete slow growing alpine species (person. Communication Hiltbrunner; Bassin et al. 2012).

Overall, the main feature of the snow cover is its insulating effect. It keeps soil temperatures above the freezing point and thus sustains the activity of microbes (e.g., O’Lear and Seastedt 1994; Hobbie and Chapin 1996; Baptist et al. 2010a) as well as of the mesofauna (Addington and Seastedt 1999). An unstable snow cover and soil freezing may thus prevent litter decomposition and delay the nitrogen mineralisation (Baptist et al. 2010a), while freeze-thaw cycles may boost the physical breakdown of litter (Seastedt et al. 2001). Major leaching of nitrogen with the melt-water is restricted by the immobilisation of nitrogen by microorganisms (Brooks et al. 1996, 1998; Brooks and Williams 1999; Schimel et al. 2004).

Due to the high resorption of N and other nutrients during senescence, the litter of alpine plants has a high ratio of carbon (C) compared to N (Seastedt et al. 2001). The C:N ratio is often used to describe the quality and decomposability of plant litter (e.g., Frankenberger and Abdelmagid 1985; Arnone and Hirschel 1997; Sanaullah et al. 2012). Soil temperature and soil moisture are important co-determinants for the decomposer community and for decomposition rates (Seastedt et al. 2001), but key drivers for the net mineralisation represent the substrate quality and quantity, which are related to the overall productivity of an ecosystem. Drought may slowdown the process of decomposition (Olson 1963; Moorhead and Reynolds 1993; O’Lear and Seastedt 1994; Seastedt et al. 2001) and limit the nutrient availability in the soil. This may potentially enlarge the competition for nutrients between plants and microbes (Jonasson et al. 1993, 1996; Jaeger et al. 1999; Körner 2003).

A pulse-labelling experiment with  $^{15}\text{N}$  in the Austrian Alps revealed a high residence time of nitrogen in the topsoil and plants of alpine grasslands. After almost 30 years, 45% of the N were still stored in the soil and plants, mostly in form of litter or soil organic matter (Gerzabek et al. 2004). Because of the low vertical mobility of nutrients, a desiccating topsoil may further inhibit the nutrient accessibility for plants (Körner 2003).

We installed a unique snow manipulation and summer drought experiment in the Swiss central Alps at 2500 m asl to address the combined effects of shifting snowmelt dates and summer drought on a late successional grassland. Because these alpine soils are usually saturated after snowmelt (Isard 1986), we expected that consequences of summer drought would be most severe in combination with snow removal and early snowmelt, with (1) reductions in the overall above-ground biomass production, (2) earlier senescence and (3) increased below-ground investments. Although many clones of *Carex curvula* may be younger than 200 years (De Witte et al. 2012), an age of up to 2000 or 4200 years is possible. Thus, single clones have already survived drastic climatic changes in the past (Steinger et al. 1996; De Witte et al. 2012). Therefore, we further hypothesised that (4) lowered soil moisture would primarily limit the soil nutrient availability of the grassland dominated by this sedge. To test our hypotheses 1-4, we examined the combined effects summer drought and early or late snowmelt on the above-ground phytomass and the root production, on litter decomposition in the soil, and on the nitrogen uptake of *Carex curvula*.

## Material and Methods

### Study site

The study site was located at 2500 m asl near the Furka pass in the Swiss central Alps (46° 33’ 47” N, 8° 23’ 28” E). With only 10° inclination, the terrain was relatively flat and featured optimal

conditions for an alpine snow manipulation and drought experiment. The dominant species was the sedge *Carex curvula*, with other frequently occurring grasses such as *Agrostis rupestris*, *Anthoxanthum alpinum* and *Helictotrichon versicolor*, as well as the forbs *Geum montanum*, *Leontodon helveticus*, *Potentilla aurea*, *Sibbaldia procumbens* and the N<sub>2</sub> fixing forb *Trifolium alpinum*. The main rooting horizon in the podsol with sandy loam was found at a depth of around 15-20 cm, but single roots could be found at up to 1 m soil depth. The year-round weather station on the close by Furkapass ([www.alpfor.ch](http://www.alpfor.ch)) recorded mean annual air temperatures of 0.3 °C (2016-2018) and mean summer temperatures (Jun-Aug) of 8.0 °C. The mean annual precipitation (2016-2018) was 1085 mm (with an estimated under-catch of snow of 200-350 mm because of strong winds in winter) and the average summer precipitation (Jun-Aug) was 365 mm.

### Experimental design and treatments

We applied the snow manipulations and summer droughts on the alpine grassland in a fully factorial design: snow manipulation (control, addition, removal of snow) was combined with summer drought (control, 5-wk moderate drought, 10.5-wk intense drought). We randomly selected 45 grassland parcels (2 x 2.5 m), organised in five replicated blocks, resulting in eight treatment levels and one control per block.

Snow manipulations were conducted few weeks before natural snowmelt, in early June 2016, in late May 2017 and in mid-June 2018. Due to unstable weather with recurrent thunderstorms in 2018, the site could be accessed in mid-June, when the snow layer was already thin. We aimed at advancing snowmelt by reducing the snowpack by snow shovelling. In 2016 and 2017, we lowered the snowpack from  $\geq 1$  m to 0.5 m, and in 2018, we reduced it from 0.5 m to 0.3 m. In order to delay snowmelt, we piled up snow to 2.2-2.5 m (2016, 2017). In June 2018, we mounted it up to 0.5-0.7 m and the snow piles were then covered with white, water permeable fleece to increase the albedo (Datex KN25, Fritz Landolt AG, CH). The fleece was removed when snow piles were 30 cm high (ten days later).

The summer drought treatment, established by rainout shelters started as soon as all parcels were snow-free: on June 16<sup>th</sup>, 2017 and on July 2<sup>nd</sup>, 2018 (no drought treatment in the year 2016 yet). The tent-like rainout shelters with a basal area of 2.5 x 3 m and a ridge height of 1.2m were centred over the parcel (2 x 2.5 m). Both long-sides of the shelters were covered with UV-B permeable foil (Lumisol AF clear, Hortuna AG, CH) to screen parcels from precipitation. Rainwater of the shelter was drained outside the lower end of the parcel (by wooden strips at the lower edge of both long sides). To minimize any microclimatic effects of the shelters, the two triangular openings were in the main wind direction (W-E). We defined a boundary zone of 20 cm width at the edges of the parcel, where we did not take any measurements and a central drought plot of 1 m<sup>2</sup> without any destructive measurements.

During the dry summer 2018, we manually watered the controls twice with 17 L m<sup>-2</sup> each (1<sup>st</sup> and 28<sup>th</sup> of August), because we observed wilting plants adjacent to our study site.

### Measurements

#### *Microclimate and weather*

During the growing seasons 2017 and 2018, two weather stations recorded air temperature, precipitation, relative humidity and wind speed at 1.5 m above the ground (Vantage Pro2, Davis Instruments Corp., USA, logging interval of 10 min). Soil temperatures at 3-4 cm depth were measured every hour (HOBO UTBI-001 TidbiT v2 Temp, Onset, US; Oct 2015 to Sep 2018) in the centre of each plot. As soon as the insulating snow disappeared, the start of daily soil temperature

fluctuations revealed the exact snowmelt date of each plot. A webcam took up to six daily pictures of our field site (<https://www.webcam-4insiders.com/de/Oberwald/15221-Oberwald.php>), letting us observe the development of the snow cover. Approximately every week during the growing seasons 2017 and 2018, we manually measured volumetric soil water content at 0-5 cm depth at five locations per plot (Theta probe ML2x, Delta-T Devices, UK). In 2018, these measurements were supplemented with measurements of volumetric soil water content at four depths in the centre of each plot: 5-10 cm, 15-20 cm, 25-30 cm, and 35-40 cm (PR2 profile probe, Delta-T Devices, UK, 35-40 cm not shown as soil moisture readings were affected by stoniness). To further characterize soil properties, we derived eight soil water retention curves at 10 cm, and seven at 30 cm soil depth (HYPROP 2, METER Environment/UMS, DE), hereafter named pF curves. pF values refer to the decadic logarithm ( $\log_{10}$ ) of the soil matrix potential. Based on the pF curves we transformed the volumetric soil water contents to pF values, which give a more appropriate measure for drought.

#### *Above-ground phytomass*

At peak biomass we harvested the current year's standing above-ground phytomass in two subplots (10 x 20 cm) of each plot (August 12<sup>th</sup>, 2017 and August 19<sup>th</sup>, 2018). The subplots in 2018 were directly adjacent to those of 2017. We kept the harvested phytomass in the fridge before dividing it into bio- and necromass. The biomass was further sorted into individual species, the necromass according to functional groups: sedge (*Carex curvula* was the only sedge), graminoids (without sedges), and forbs. Lichens were excluded as they may be several years old and a differentiation into alive and dead is impossible. After drying the phytomass samples for 24 h at 80 °C, the samples were weighed to determine the dry matter. We averaged the above-ground phytomass of the two subplots in each plot.

#### *In-growth cores*

At the start of the growing season, in late June 2017, we installed three in-growth cores per parcel, adjacent to the central 1 m<sup>2</sup> drought plot to determine the below-ground root mass. We collected soil cores with a diameter of 4.8 cm and a soil depth of 21 cm. We kept the vegetated top 2 cm to re-cover the ingrowth cores. We sieved the extracted soil (2 mm mesh size, Retsch GmbH, DE) and manually removed all roots and rhizomes. Then, we mixed the soil of all cores and re-filled the holes with the sieved root-free soil. After two growing seasons (2017, 2018) and one winter, we re-collected the in-growth cores in September 2018, by extracting slightly smaller soil cores (4.4 cm diameter, 20 cm depth). To differentiate between soil depths, we divided each 20 cm long in-growth core into an upper layer (2-10 cm soil depth), and a lower layer (10-20 cm), leaving the vegetated top 2 cm at its original location. We stored the ingrowth cores in the freezer and before further processing, we let them thaw in a fridge at 4 °C. We manually picked out all visible roots with tweezers and sieved the soil twice to extract all the remaining roots. These were carefully washed and dried at 80 °C for at least 24 h before determining the root dry matter on a microbalance (Satorius SecuraA225D-1S, DE).

#### *In-growth cores with soil nutrient layer*

Along with the in-growth cores described above, we installed in-growth cores with an additional nutrient layer in the upper half of the plots in three of the five experimental blocks. During the filling of the holes with sieved soil, we added a slow-release NPK fertilizer (Hauert, CH) in form of

powder at 5 cm soil depth, corresponding to  $10 \text{ kg N ha}^{-1} \text{ a}^{-1}$ . The NPK-fertilizer was mixed with talcum powder (Fluka, CH; 2.5 g per core) to guarantee a homogeneous fertilizer layer within each soil core.

#### *Litter decomposition*

We used litter bags to estimate the seasonal and annual decomposition of plant material in the soil. At peak biomass in 2017, we harvested above-ground phytomass, close to our experimental site. After drying the phytomass at  $80 \text{ }^\circ\text{C}$ , we cut the plant material into pieces of 2 mm, thoroughly mixed the material and filled 2.3 g into rectangular nylon mesh bags (NITEX SEFAR AG, Switzerland,  $5 \times 5.2 \text{ cm}$ , mesh size of 0.25 mm). These bags (named on-site litter bags hereafter) were then re-dried for 3 h at  $80 \text{ }^\circ\text{C}$  to determine the total dry weight.

To determine the seasonal weight loss, we buried two series of litter bags at the end of the growing season 2017 (September 22<sup>nd</sup>,  $n = 3$  per plot and series, 0-5 cm soil depth). One series was collected on July 9<sup>th</sup>, 2018 (mass loss over winter), the other series was removed from the soil on September 18<sup>th</sup>, 2018 (mass loss over one year). The litter bags of the winter series were immediately replaced with new litter bags. This summer series was recollected at the end of the growing season, together with the yearly series. Directly after recollection, litter bags were carefully cleaned and then dried at  $80 \text{ }^\circ\text{C}$ . We determined the dry mass and assessed the relative weight loss to estimate the fraction of decomposed plant litter. We excluded litter bags with holes from the dataset. To get an estimate of the decomposition of different litter types, we also buried Rooibos tea bags (2 g, Lipton, Unilever, UK, as used and described in Keuskamp et al. 2013 for a global assessment of decomposition across ecosystems). The mesh size of 0.25 mm was the same as for the on-site litter bags, but the tea bags were tetrahedron-shaped (5 cm side length).

#### *Labelling experiment*

To assess whether the nutrient uptake was limited under drought, we buried  $^{15}\text{N}$  enriched maize litter bags alongside the on-site and the Rooibos litter bags. We grew the maize plants («Golden Bantam», seeds from Zollinger, CH) in 10 L pots (6 seeds per pot) in the greenhouse of the Botanical Institute Basel. In seven additions over the course of one month, we applied 17.5 mg of dissolved, 98% enriched  $^{15}\text{N}$  ammoniumnitrate per pot. After harvesting the plants, we dried the leaves for 48 h at  $80 \text{ }^\circ\text{C}$  and cut them into pieces of 2 mm. We filled 3 g into nylon mesh bags (same material as on-site litter bags) with a dimension of  $7 \times 7.5 \text{ cm}$ . We proceeded in the same manner as with the on-site litter bags, with a winter, a yearly, and a summer series (3 maize litter bags per series and plot), and buried them at a soil depth of 0-7 cm.

To evaluate whether the products of litter decomposition and mineralisation were resorbed by the vegetation, we analysed the foliar  $\delta^{15}\text{N}$  of the sedge *Carex curvula*. In a distance of 2 and 5 cm to the maize litter bags, we harvested the two youngest *C. curvula* leaves formed during this growing season. A first harvest took place on July 16<sup>th</sup>, 2018. We performed a second harvest on September 19<sup>th</sup>, 2018, after the removal of all maize litter bags (summer series). Because we had placed the summer series in the same location as the winter series, the *C. curvula* plants were exposed to twice the amount of labelled maize leaves.

#### *Foliar isotopic composition of C. curvula*

For the analysis of the foliar isotopic composition, we cut the dried *C. curvula* leaves into small pieces of 1 mm and weighed 1.9 mg into tin capsules. The samples were then analysed on a Flash

2000 elemental analyser (EA; for % N and % C) coupled to a Thermo Finnigan Delta Plus XP isotope ratio mass spectrometer (IRMS) via a ConFlo IV interface (both Thermo Fisher Scientific, DE).  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values were normalized to the known standards of AIR- $\text{N}_2$  and VPDB, respectively. The analytical precision calculated from the standard deviation of repeat analyses of quality control standards was 0.05‰ for  $\delta^{15}\text{N}$  values and 0.08‰ for  $\delta^{13}\text{C}$  values. The isotopic composition of young *C. curvula* leaves in the above-ground phytomass harvest of 2018 served as a reference for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values.

### Statistical analyses

We analysed the effect of the snow manipulations and the drought treatments on the above-ground phytomass, on root mass, on the litter decomposition, and nutrient uptake using linear mixed models with random intercepts for the five replicate blocks (R package lme4 v. 1.1.21, Bates et al. 2020).

#### *Treatment effects*

We assessed effects of the snow manipulations, summer droughts and the two years on the above-ground phytomass. We allowed for all interaction effects (model: snow x drought x year,  $n = 5$  random blocks). Biomass, necromass and weekly biomass formation were analysed in the same manner. We also evaluated the treatment effects for both years and for each functional group separately. The response variable was square root transformed to fulfil the model assumptions of linear regression.

For the root mass grown into the in-growth cores ( $\text{g m}^{-2}$ ), we took the two different soil layers into account (2-10 and 10-20 cm; model: snow x drought x depth,  $n = 5$  random blocks). Prior to the analysis, we corrected for the different core lengths by multiplying the root mass of the lower layer by 0.8 (volume correction). To test whether the additional nutrient layer affected the root production, we included the NPK addition in the model above (model: snow x drought x depth x nutrient,  $n = 3$  random blocks). The root mass values were square root transformed for all analyses.

We evaluated how the litter decomposition was affected by the experimental treatments over the different seasons (winter, year, summer; model: snow x drought x season,  $n = 5$  random blocks). Accordingly, we repeated these statistics for the maize litter bags. We then estimated the treatment effects on the nitrogen uptake of *C. curvula*, by analysing the shifts in foliar  $\delta^{15}\text{N}$  values, for two distances (2 and 5 cm), and for three seasons (winter, year, summer; (model: snow x drought x season,  $n = 5$  random blocks), as well as for each season separately.

The residuals of all statistical models were checked visually and whenever appropriate, we performed stepwise backwards model selection. Significant effects on the response variable were tested with an ANOVA (R package car, v 3.0.6, John et al., 2020). All within-treatment comparisons were assessed by Tukey post-hoc contrasts of the R package emmeans (v.1.4.5, Lenth et al. 2019) and the  $R^2$  was computed according to Nakagawa and Schielzeth (2013). Group means are given with their associated standard deviations (sd) or are presented with standard errors (se) in case for figures. All statistical analyses were performed with the statistical software R (R Core Team 2019).

### Within treatment variability

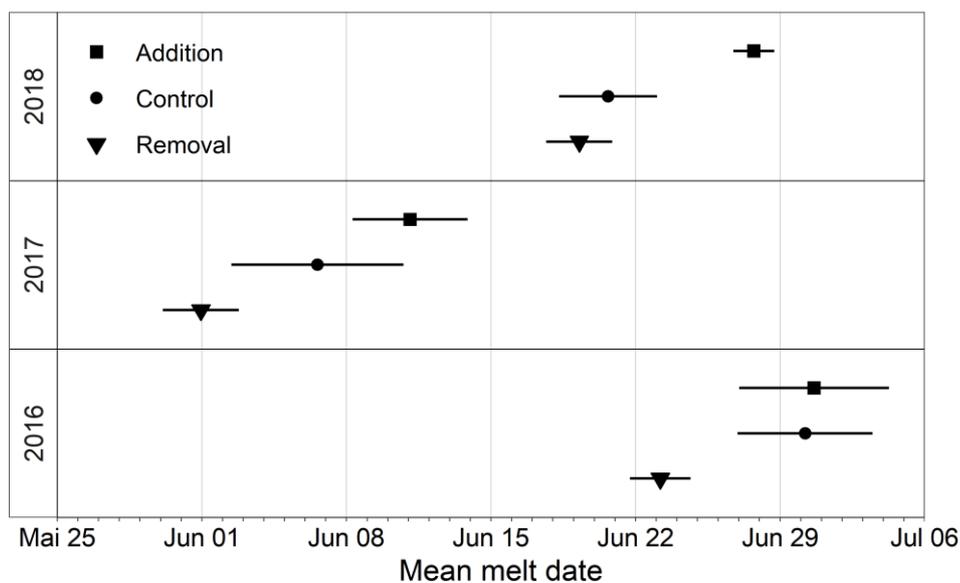
For above-ground phytomass and root mass analyses, as well as for the evaluation of the litter decomposition, we additionally calculated statistical models that accounted for the within-treatment variability. For the drought treatment we assessed the effect of the mean pF value over the growing season ( $pF_{\text{mean}}$ ), for the snow manipulations we evaluated the effect of degree days (DD: daily mean soil temperature exceeding a threshold of 0 °C or 5 °C, respectively, during the period after snowmelt until harvest/recollection). As these continuous predictors for drought or snow manipulations did not explain a higher proportion of the variance than the experimental categories, we do not report these results.

## Results

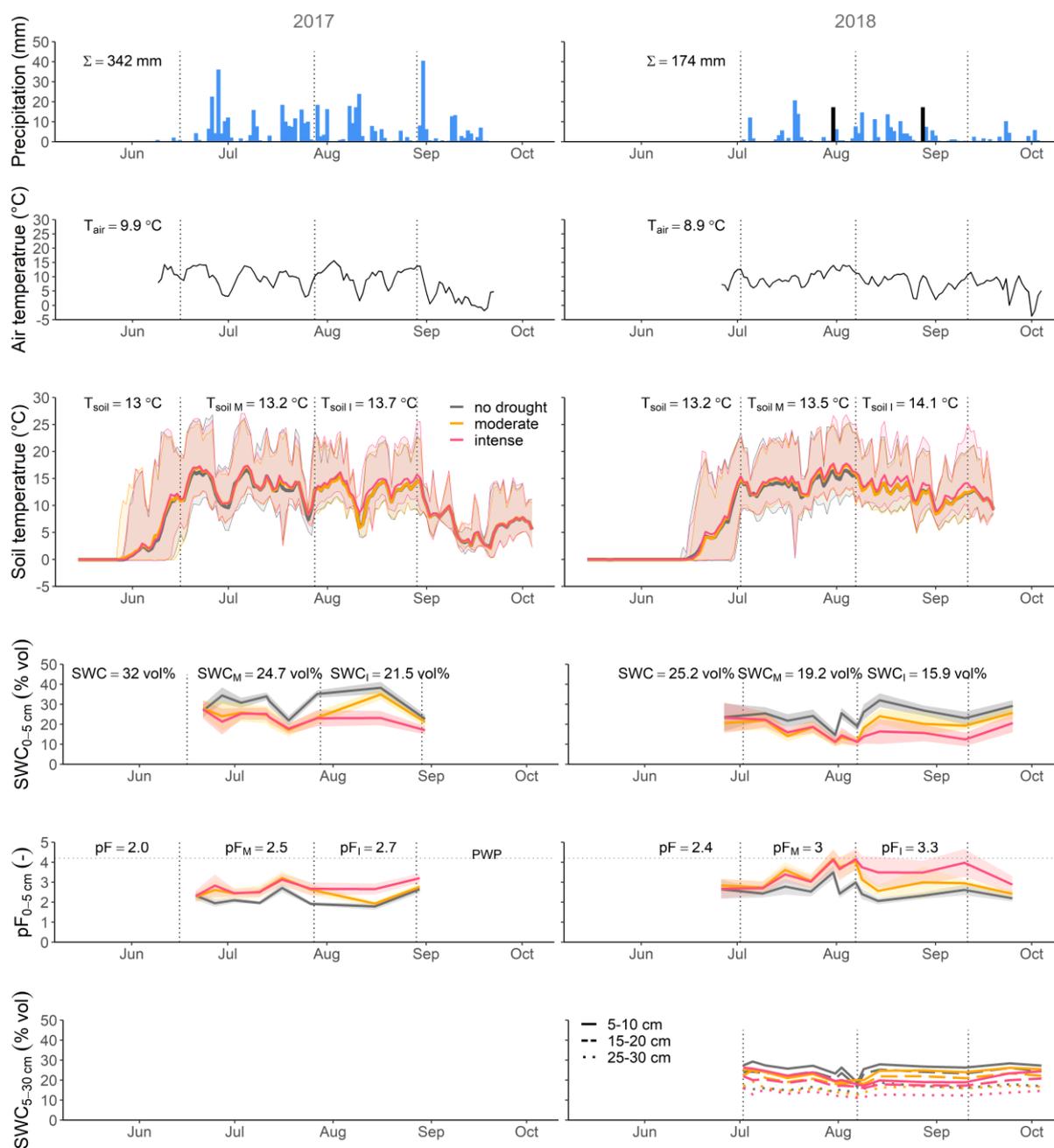
### Snow cover and snowmelt dates

The onset of a continuous snow cover in both winters 2016/17 and 2017/18 started in November. In the winter 2016/17, a well-developed snow cover was formed very late, at the beginning of February, one year later it was already developed in mid-December. In both winters, sub-zero temperatures were measured in the month before a well-insulating snow cover was formed, with a minimum of -6.6 °C in January 2017 (mean across plots) and -2.8 °C in December 2017, respectively.

The annual variability in the natural snowmelt dates across the three years was large: median snowmelt dates on controls were July 1<sup>st</sup> in 2016, June 7<sup>th</sup> in 2017, and June 21<sup>st</sup> in 2018 (Figure 3.1). Snow addition delayed the snowmelt by one day in 2016, by four days in 2017 and by six days in 2018 (median). While we achieved to advance snowmelt by nine days in 2016 and by six days in 2017, the snow removal was less effective in 2018, as there was a two-day difference compared to the median snowmelt dates of the controls.



**Figure 3.1** Snowmelt date (mean  $\pm$  sd) of three consecutive years (2016-2018) with snow manipulation (see Chapter 2)



**Figure 3.2** Weather conditions and treatment effects at the study site, with daily precipitation, daily mean air temperatures, daily mean, minimum and maximum soil temperatures, regularly assessed soil water contents ( $SWC \pm se$ ) and pF values ( $\pm se$ ). Colours of the soil temperature, soil water content and pF refer to the drought treatments. Numbers above the plot indicate precipitation sums, mean temperatures, and median SWC/pF of the control, the moderate drought treatment (M) and the intense drought treatment (I) for the total period of the intense drought treatment (10.5 weeks). Black bars in the precipitation data indicate manual watering of the controls in 2018

## Drought

The drought treatment effectively reduced volumetric soil water contents at 5 cm and down to a soil depth of 30 cm (Figure 3.2) during the two treatment periods (2017, 2018). The natural precipitation during the moderate drought amounted 205 mm and 68 mm in 2017 and 2018, respectively. During the subsequent second half of the intense drought, another 137 mm (2017) and 106 mm (2018) were excluded by the shelters. In 2017, the  $pF_{\text{median}}$  of controls was 2.0 (0-5

cm soil depth, corresponding to 32.0 vol% SWC). During the 5-wk moderate drought it was 2.6 (22.6 vol%), recovering to levels of the controls after removing the rainout shelters (Figure 3.2). Under intense drought, the  $pF_{\text{median}}$  was 2.7 (21.5 vol%). The year 2018 was generally drier, with a  $pF_{\text{median}}$  of 2.4 (25.2 vol%) in the controls. Thus, despite the watering of controls in 2018, they were overall similarly dry as in the moderate drought treatment of 2017. Temporarily, the controls of 2018 were even drier than the intense drought plots of 2017. The  $pF_{\text{median}}$  was 3.2 (17.2 vol%) during the 5-wk moderate drought and 3.3 (15.9 vol%) for the intense drought in 2018. Around the beginning of August 2018, the permanent wilting point ( $pF$  4.2 at a volumetric soil water content of  $10.1 \text{ vol}\% \pm 1.5 \text{ vol}\%$  at 10 cm soil depth;  $pF$  curves in Figure S3.1 of *Supplemental material*) was reached by several plots of both drought treatments ( $pF_{0-5\text{cm}}$  in Figure 3.2). The soil moisture and also the treatment effect decreased with the soil depth (SWC in Figure 3.2). The rainout shelters further had a warming effect, evidenced by higher soil temperatures. These mainly manifested as higher daily minimum temperatures (mean increase of 1.1 K), as the shelters reduced radiative cooling during clear nights. During the period of the moderate drought, daily mean temperatures were 0.5 K higher in 2017 and 0.9 K higher in 2018. During the second half of the intense drought, this increase was 0.9 K in both years (Figure 3.2). On August 11<sup>th</sup> 2017, the rainout shelters screened snow from falling directly on the intense drought parcels and kept the daily mean soil temperatures at 8.7 °C, compared to 6.0 °C in the controls. The snow manipulations did not affect the soil water content beyond two weeks after the start of the drought treatment in 2017, and 3 weeks in 2018 (taken from the weekly measurements at 0-5 cm soil depth).

### Above-ground phytomass

#### *Phytomass*

During the growing season 2017 with early snowmelt and higher water availability, roughly 30% more phytomass were produced ( $179.2 \pm 46.5 \text{ g m}^{-2}$ , across all snow manipulations without drought) than during 2018 ( $125.1 \pm 26.1 \text{ g m}^{-2}$ ,  $p < 0.01$ , Figure 3.3).

The growing season 2018 started later but was rather dry. The snow manipulations did not affect the phytomass formation ( $p = 0.69$ ), but there was a marginal drought effect across both years ( $p = 0.09$ ). Intense drought reduced the above-ground phytomass by 6% in 2017 ( $10.8 \text{ g m}^{-2}$ ), and by 16% in 2018 ( $20.8 \text{ g m}^{-2}$ ,  $p = 0.05$ ), but there was no significant interaction between years and drought ( $p = 0.34$ , Table 3.1). The two years and the drought treatment together explained 40% of the variability in the harvested above-ground phytomass. The  $pF_{\text{median}}$  and growing degree days ( $DD \geq 5^\circ\text{C}$ ) did not increase the explanatory power of the statistical model.

All three functional groups produced more above-ground phytomass in 2017 than 2018 ( $p < 0.01$ , Figure 3.3). The overall phytomass was strongly affected by the dominant *C. curvula* as it accounted for roughly 50% of the dry matter. Its phytomass was 30% higher in 2017 ( $89.7 \pm 15.8 \text{ g m}^{-2}$  on controls) than in 2018 ( $61.8 \pm 9.8 \text{ g m}^{-2}$ ,  $p < 0.01$ ). *C. curvula*'s response to the treatments differed between years, with no effect in 2017 ( $p_{\text{drought}} = 0.41$ ,  $p_{\text{snow}} = 0.24$ ), but a pronounced response to drought in 2018 ( $p_{\text{drought}} = 0.04$ ,  $p_{\text{snow}} = 0.95$ ). Without drought in 2018, the mean above-ground phytomass of *C. curvula* was  $60.5 \pm 11.2 \text{ g m}^{-2}$ , whereas it slightly decreased by 7% to  $56.2 \pm 18.6 \text{ g m}^{-2}$  under intense drought. Under moderate drought it increased by 20% (to  $72.3 \pm 22.3 \text{ g m}^{-2}$ ; Figure 3.4).

Similarly, the intense drought in 2018 reduced the phytomass of forbs by 25% ( $p = 0.03$ ), from  $46.6 \pm 16.7 \text{ g m}^{-2}$  to  $35.0 \pm 12.4 \text{ g m}^{-2}$  (Table 3.1). The graminoids (without sedges), accounting for 14% of the total phytomass (Figure 3.3), were the only functional group with a significant

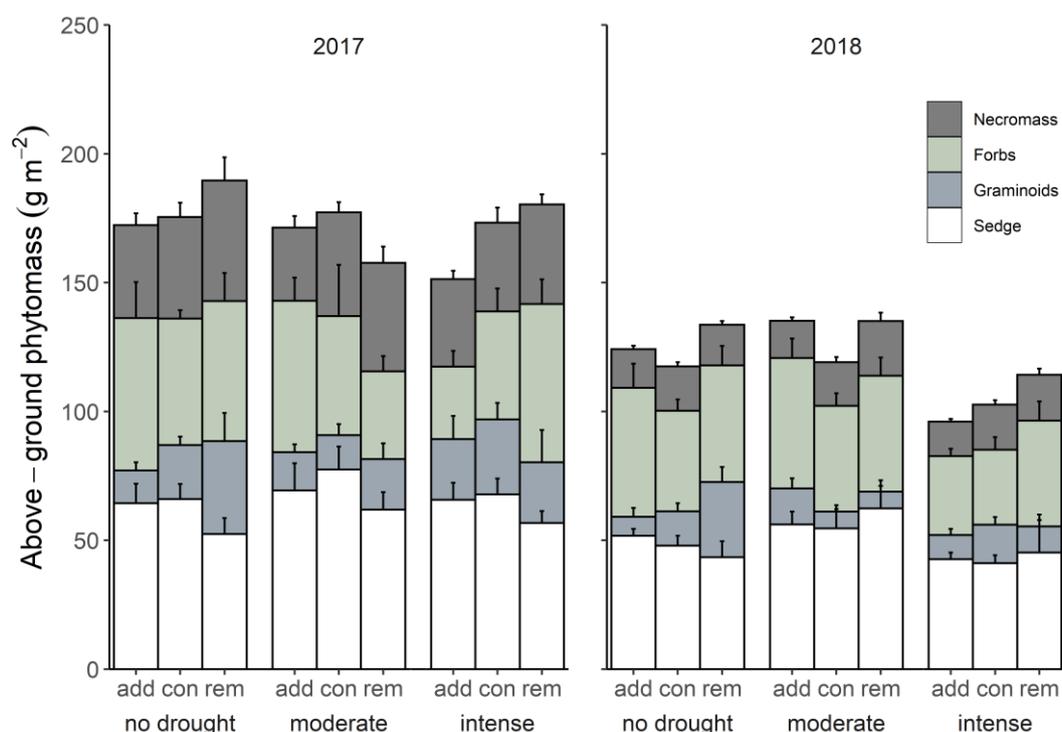
interaction between the drought treatment and the snow manipulations in 2018 ( $p = 0.05$ ). However, this interaction effect was most likely due to a high abundance of the grasses *Helictotrichon versicolor* and *Nardus stricta* in two of the plots with snow removal and without drought.

### Biomass and necromass

Similar to the total phytomass, the biomass was 22% higher in 2017 ( $138.4 \pm 33.0 \text{ g m}^{-2}$ , plots without drought) than in 2018 ( $109.1 \pm 25.7 \text{ g m}^{-2}$ ). The intense drought in 2018 significantly reduced the biomass by 19% ( $p = 0.03$ ), whereas there was no effect of the moderate drought treatment ( $p = 0.91$ ) or of the snow manipulations ( $p = 0.82$ ).

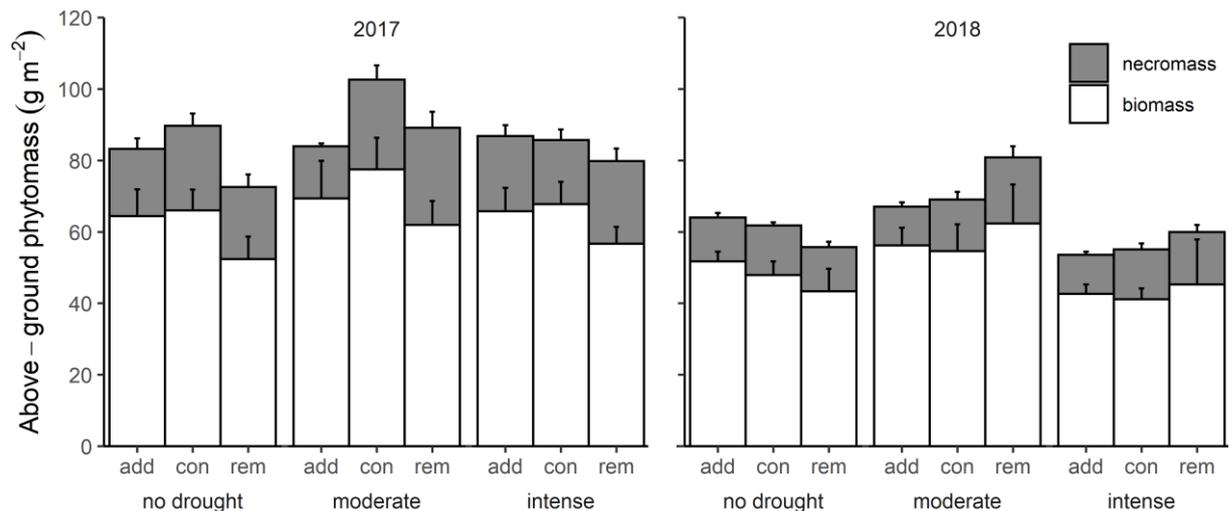
The necromass on controls amounted  $39.4 \pm 12.5 \text{ g m}^{-2}$  in 2017, and  $17.2 \pm 3.4 \text{ g m}^{-2}$  in 2018, accounting for 22% (2017) and 15% (2018) of total phytomass, respectively. The absolute amount of necromass was unaffected by the drought treatments ( $p = 0.51$ ) but differed between snow manipulations ( $p < 0.01$ ). The snow addition reduced the necromass in both years, by 14% but non-significant ( $p = 0.35$ ) in 2017 and by 17% ( $p = 0.01$ ) in 2018. Snow removal on the other hand increased the amount of necromass by 12% ( $p = 0.47$ ) and 6% ( $p = 0.64$ ), respectively.

For the dominant *C. curvula*, we assessed  $66.1 \pm 13.0 \text{ g m}^{-2}$  biomass and  $23.6 \pm 7.7 \text{ g m}^{-2}$  necromass in 2017, and  $47.9 \pm 8.6 \text{ g m}^{-2}$  biomass vs.  $13.8 \pm 2.1 \text{ g m}^{-2}$  necromass in 2018. The snow removal in 2017 significantly reduced the biomass by 5% ( $p = 0.05$ ). We only observed a response to the drought treatment in 2018 ( $p = 0.02$ ), with a 9% increase in biomass under moderate drought, and a 17% decrease under intense drought. Neither snow manipulations ( $p = 0.11$ ) nor the drought treatments ( $p = 0.79$ ) affected the amount of *C. curvula*'s necromass in 2017. In 2018, snow addition reduced the necromass by  $2.7 \text{ g m}^{-2}$  on average ( $p = 0.02$ ), whereas all other treatments had no significant effect.



**Figure 3.3** Above-ground phytomass (dry matter,  $\text{g m}^{-2}$ ) sorted into biomass of functional groups and total necromass (mean + 1 se,  $n = 5$ ) for the snow manipulations and drought treatments ( $n = 5$ ). The dominant sedge *C. curvula* is presented separately, thus, graminoids are without sedges

The graminoid's biomass (Table 3.1) was largely unaffected by both treatments, snow manipulation and summer drought, but under intense drought in 2018, there was slightly more necromass ( $p = 0.08$ ; Table 3.1). In contrast to all other functional groups, the biomass of forbs was similar in both years ( $p = 0.17$ , Table 3.1). Nevertheless, the intense drought treatment in 2018 reduced their biomass by 25%. The forb's necromass was significantly higher in 2017 ( $p < 0.01$ ), but it was unaffected by the treatments.



**Figure 3.4** Phytomass in  $\text{g m}^{-2}$  (bio- and necromass, mean + 1 se) of the dominant species *C. curvula*, for the snow manipulations and drought treatments ( $n = 5$ )

#### *Weekly biomass formation*

To account for the fact that the growing season 2017 was 3.5-wk longer than in 2018, we also analysed the biomass formation per snow-free week: on controls it was 21% higher in 2017 than in 2018 (Table 3.2). The analysis of single years revealed no treatment effects in 2017, but a significant reduction by 20% under intense drought in 2018 (mean reduction of  $2.8 \text{ g m}^{-2} \text{ wk}^{-1}$ , across snow manipulations,  $p < 0.01$ ), as well as an enhanced biomass formation by 19% after snow addition (mean increase across drought treatments of  $2.6 \text{ g m}^{-2} \text{ wk}^{-1}$ ,  $p = 0.05$ ). Thus, the analysis of biomass formation rates disclosed similar drought effects as for the overall biomass production but revealed the higher formation rates after early snowmelt.

Also *C. curvula* had a 22% higher weekly biomass formation in 2017 than in 2018 (Table 3.2). In contrast to the total phytomass, the weekly biomass formation of *C. curvula* was significantly reduced by 25% after snow removal in 2017 (mean reduction of  $1.9 \text{ g m}^{-2} \text{ wk}^{-1}$ ,  $p = 0.01$ ). Even though we observed a similar pattern in 2017, there was a significant effect of the drought treatment on the biomass formation in 2018 only: moderate drought increased the biomass formation by 20% (increase of  $1.2 \text{ g m}^{-2} \text{ wk}^{-1}$ ), whereas intense drought decreased it by 11% (mean reduction of  $0.6 \text{ g m}^{-2} \text{ wk}^{-1}$ ).

The biomass formation in graminoids was 31% higher in 2017 ( $2.3 \pm 0.7 \text{ g m}^{-2}$  on controls) than in 2018 ( $1.6 \pm 0.9 \text{ g m}^{-2}$ ,  $p = 0.01$ ). Again, the high proportion of graminoids in two parcels with snow removal and without drought treatment caused a significant interaction of the drought treatments and snow manipulations ( $p < 0.01$ ). Only in the forbs, the weekly biomass formation was not significantly higher in 2017 ( $5.4 \pm 0.7 \text{ g m}^{-2} \text{ wk}^{-1}$ , controls) than 2018 ( $4.6 \pm 1.2 \text{ g m}^{-2}$ ,  $p = 0.75$ , data not shown). Nevertheless, under intense drought their biomass formation rate decreased by 26% in 2018 ( $p = 0.08$ ).

**Table 3.1** Total phytomass, biomass and necromass in g m<sup>-2</sup>(mean ± sd) for the years 2017 and 2018, separated by functional groups. The full control is shaded in grey

Drought		Snow		Phytomass		Biomass		Necromass	
		2017	2018	2017	2018	2017	2018	2017	2018
none	add	172.3 ± 35.8	124.2 ± 24.8	136.3 ± 26.2	109.2 ± 24.6	36.1 ± 10.2	15.0 ± 3.0		
	cont	175.5 ± 28.5	117.5 ± 12.4	136.1 ± 18.6	100.3 ± 10.5	39.4 ± 12.5	17.2 ± 3.4		
	rem	189.7 ± 72.5	133.7 ± 38.0	142.9 ± 52.4	117.9 ± 37.6	46.8 ± 20.2	15.8 ± 3.2		
mod	add	171.4 ± 46.9	135.2 ± 29.1	142.9 ± 43.3	120.7 ± 26.4	28.5 ± 10.1	14.4 ± 3.1		
	cont	177.3 ± 38.9	119.2 ± 14.4	137.0 ± 37.0	102.2 ± 10.9	40.3 ± 8.8	17.0 ± 4.4		
	rem	157.7 ± 23.1	135.1 ± 36.4	115.6 ± 9.4	113.9 ± 29.1	42.1 ± 14.1	21.2 ± 7.4		
int	add	151.3 ± 28.1	96.0 ± 11.2	117.4 ± 21.0	82.7 ± 12.2	33.9 ± 7.3	13.4 ± 2.3		
	cont	173.3 ± 49.9	102.7 ± 18.2	138.8 ± 41.7	85.2 ± 16.8	34.4 ± 13.0	17.5 ± 3.7		
	rem	180.4 ± 36.4	114.3 ± 37.1	141.7 ± 32.1	96.5 ± 32.8	38.7 ± 8.7	17.8 ± 5.3		

***C. curvula***

none	add	83.2 ± 23.2	64.0 ± 8.3	64.4 ± 16.8	51.7 ± 6.1	18.8 ± 6.6	12.3 ± 2.9		
	cont	89.7 ± 15.8	61.8 ± 9.8	66.1 ± 13.0	47.9 ± 8.6	23.6 ± 7.7	13.8 ± 2.1		
	rem	72.6 ± 20.4	55.7 ± 15.0	52.4 ± 14.0	43.4 ± 14.1	20.2 ± 7.8	12.3 ± 3.4		
mod	add	84.0 ± 25.0	67.0 ± 13.6	69.3 ± 23.6	56.2 ± 11.1	14.7 ± 1.7	10.8 ± 2.7		
	cont	102.7 ± 28.2	69.1 ± 21.4	77.5 ± 19.9	54.6 ± 16.8	25.2 ± 8.8	14.5 ± 4.8		
	rem	89.1 ± 24.4	80.9 ± 31.0	61.9 ± 15.0	62.3 ± 24.4	27.2 ± 10.0	18.5 ± 6.9		
int	add	86.8 ± 20.8	53.6 ± 5.9	65.8 ± 14.7	42.7 ± 5.8	21.1 ± 6.9	10.9 ± 2.0		
	cont	85.7 ± 17.1	55.1 ± 10.1	67.8 ± 13.9	41.2 ± 6.7	17.9 ± 6.7	13.9 ± 3.8		
	rem	79.9 ± 17.6	59.9 ± 32.4	56.7 ± 10.4	45.3 ± 28.2	23.2 ± 7.8	14.6 ± 4.5		

***Forbs***

none	add	70.0 ± 41.4	52.0 ± 22.3	59.1 ± 31.2	50.1 ± 20.9	10.9 ± 10.3	2.0 ± 2.2		
	cont	58.7 ± 10.8	41.3 ± 11.0	49.1 ± 7.2	39.1 ± 9.7	9.5 ± 4.6	2.2 ± 1.7		
	rem	70.1 ± 32.1	46.5 ± 17.0	54.4 ± 24.3	45.3 ± 16.9	15.8 ± 8.2	1.2 ± 0.6		
mod	add	67.7 ± 23.9	53.0 ± 17.7	58.8 ± 20.1	50.6 ± 16.9	9.0 ± 6.3	2.4 ± 1.5		
	cont	56.3 ± 49.7	42.7 ± 10.9	46.2 ± 44.5	41.1 ± 10.8	10.1 ± 5.7	1.6 ± 0.8		
	rem	44.0 ± 17.6	47.2 ± 16.6	34.1 ± 13.2	45.0 ± 15.7	9.9 ± 4.8	2.1 ± 1.1		
int	add	33.6 ± 18.5	31.5 ± 6.7	28.2 ± 13.7	30.6 ± 6.3	5.4 ± 5.2	0.8 ± 0.9		
	cont	50.6 ± 24.4	30.8 ± 10.2	41.9 ± 19.8	29.1 ± 10.9	8.7 ± 4.7	1.7 ± 1.5		
	rem	71.3 ± 21.7	42.6 ± 16.6	61.4 ± 21.4	41.0 ± 16.7	9.9 ± 1.2	1.5 ± 0.8		

***Graminoids***

none	add	19.1 ± 9.6	8.1 ± 8.2	12.7 ± 6.9	7.4 ± 7.8	6.4 ± 2.7	0.7 ± 0.8		
	cont	27.1 ± 6.3	14.5 ± 7.5	20.9 ± 7.4	13.3 ± 7.2	6.3 ± 2.5	1.2 ± 0.7		
	rem	46.9 ± 30.0	31.4 ± 13.7	36.1 ± 24.3	29.2 ± 13.2	10.8 ± 6.7	2.2 ± 0.7		
mod	add	19.7 ± 10.8	15.1 ± 9.8	14.8 ± 7.0	13.9 ± 8.7	4.9 ± 4.5	1.2 ± 1.1		
	cont	18.4 ± 10.6	7.3 ± 6.4	13.3 ± 9.7	6.5 ± 5.7	5.0 ± 2.2	0.8 ± 0.8		
	rem	24.6 ± 12.9	7.1 ± 5.5	19.6 ± 13.8	6.5 ± 5.1	5.0 ± 1.9	0.6 ± 0.5		
int	add	30.9 ± 25.8	11.0 ± 6.6	23.5 ± 20.1	9.4 ± 5.4	7.4 ± 6.3	1.6 ± 1.7		
	cont	37.0 ± 15.9	16.8 ± 6.9	29.2 ± 14.2	14.9 ± 6.5	7.9 ± 5.0	1.9 ± 1.1		
	rem	29.2 ± 31.6	11.8 ± 11.3	23.6 ± 28.0	10.1 ± 10.3	5.6 ± 3.6	1.6 ± 1.1		

**Table 3.2** Weekly biomass production in  $\text{g m}^{-2} \text{wk}^{-1}$  (mean  $\pm$  sd) across treatments 2017 and 2018. The full control is shaded in grey

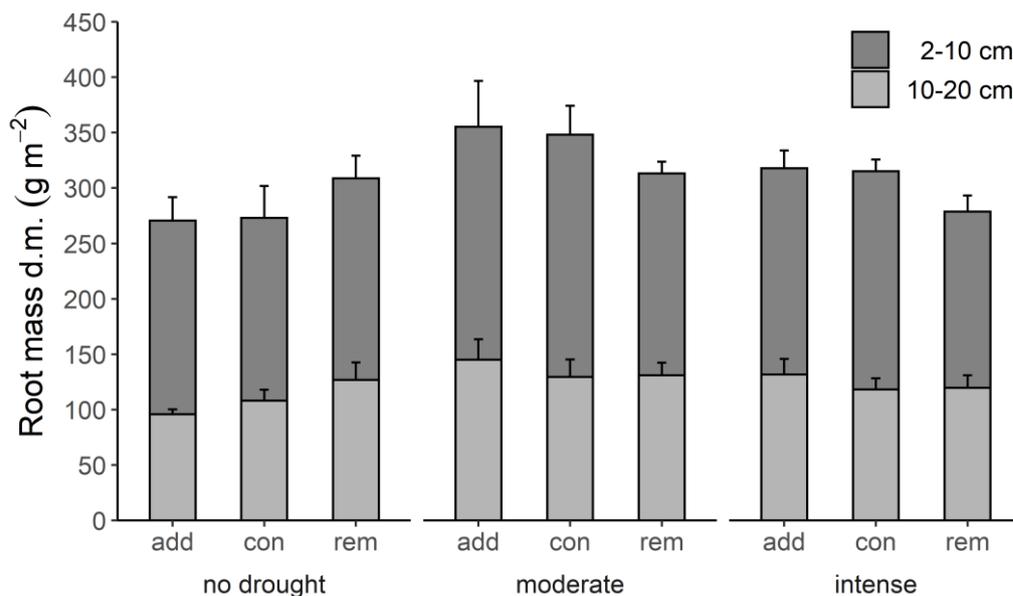
Drought treatment	Snow manipulation	2017	2018	2017	2018
		Biomass formation total ( $\text{g m}^{-2} \text{wk}^{-1}$ )	Biomass formation total ( $\text{g m}^{-2} \text{wk}^{-1}$ )	<i>C. curvula</i> biomass formation ( $\text{g m}^{-2} \text{wk}^{-1}$ )	<i>C. curvula</i> biomass formation ( $\text{g m}^{-2} \text{wk}^{-1}$ )
control	addition	16.2 $\pm$ 3.2	14.8 $\pm$ 3.5	7.7 $\pm$ 2.2	6.9 $\pm$ 0.7
	control	15.0 $\pm$ 1.8	11.9 $\pm$ 1.5	7.3 $\pm$ 1.6	5.7 $\pm$ 1.2
	removal	14.4 $\pm$ 5.3	13.7 $\pm$ 4.5	5.3 $\pm$ 1.4	5.0 $\pm$ 1.5
moderate	addition	16.9 $\pm$ 5.5	16.4 $\pm$ 3.4	8.3 $\pm$ 3.0	7.6 $\pm$ 1.2
	control	14.5 $\pm$ 4.3	12.0 $\pm$ 1.2	8.2 $\pm$ 2.0	6.4 $\pm$ 1.9
	removal	11.4 $\pm$ 0.7	13.3 $\pm$ 3.3	6.0 $\pm$ 1.3	7.3 $\pm$ 2.7
intense	addition	13.6 $\pm$ 2.3	10.9 $\pm$ 1.9	7.6 $\pm$ 1.7	5.6 $\pm$ 0.8
	control	15.2 $\pm$ 4.8	10.2 $\pm$ 2.0	7.3 $\pm$ 1.6	4.9 $\pm$ 0.7
	removal	14.2 $\pm$ 3.3	11.1 $\pm$ 3.6	5.7 $\pm$ 1.0	5.2 $\pm$ 3.0

### Below-ground root mass and the effect of a nutrient layer

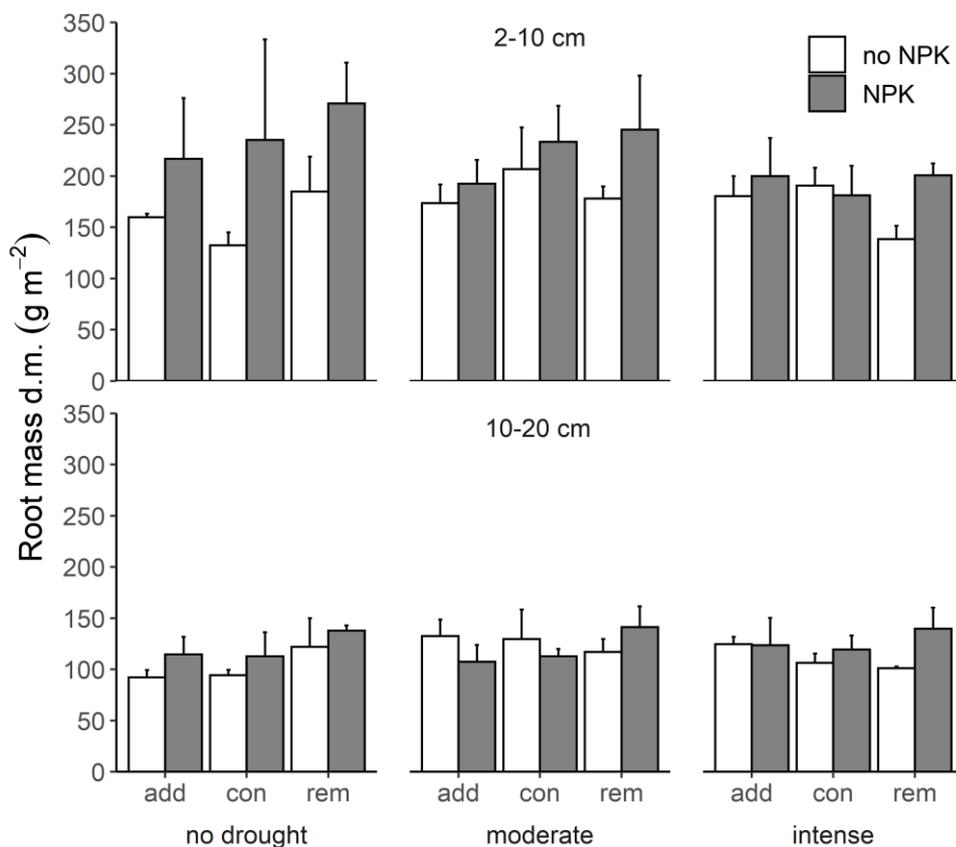
After two growing seasons and one winter (2017 / 2018), we exclusively found fine roots in the in-growth cores, but no newly formed rhizomes. The root mass of  $164.9 \pm 64.5 \text{ g m}^{-2}$  in the upper layer (2-10 cm) of the in-growth in controls cores was substantially higher than in the lower layer (10-20 cm) with  $108.2 \pm 21.6 \text{ g m}^{-2}$  ( $p < 0.01$ , Figure 3.5). Moderate drought increased the total root mass ( $p = 0.01$ ) by 19% or  $54.7 \text{ g m}^{-2}$ , corresponding to a  $29.8 \text{ g m}^{-2}$  increase in the upper layer and  $24.9 \text{ g m}^{-2}$  in the lower layer. Intense drought yielded similar amounts of roots as in the controls ( $+6.8 \text{ g m}^{-2}$  in the upper layer,  $+12.9 \text{ g m}^{-2}$  in the lower layer,  $p = 0.40$ ). In both soil layers the snow manipulations did not affect the root mass ( $p = 0.84$ ).

The nutrient layer at 5 cm soil depth significantly increased the root mass by 77.7% ( $102.8 \text{ g m}^{-2}$ ) in the upper layer of controls, and by 42.7% ( $40.2 \text{ g m}^{-2}$ ) in the lower layer ( $p < 0.01$ ). There was no statistically significant interaction effect with snow manipulations ( $p = 0.20$ ), but we saw a slight trend of an interaction with drought ( $p = 0.11$ ). Without snow manipulations, the nutrient induced increase in the root mass under drought was only 12.9% under moderate drought, and -5.1% under intense drought. The in-growth cores were installed after the snow manipulations in 2017 and the snow removal in 2018 advanced snowmelt by two days only. Nevertheless, in combination with a nutrient layer, the root mass of the in-growth core was always highest in parcels with snow removal (both soil layers; Figure 3.6).

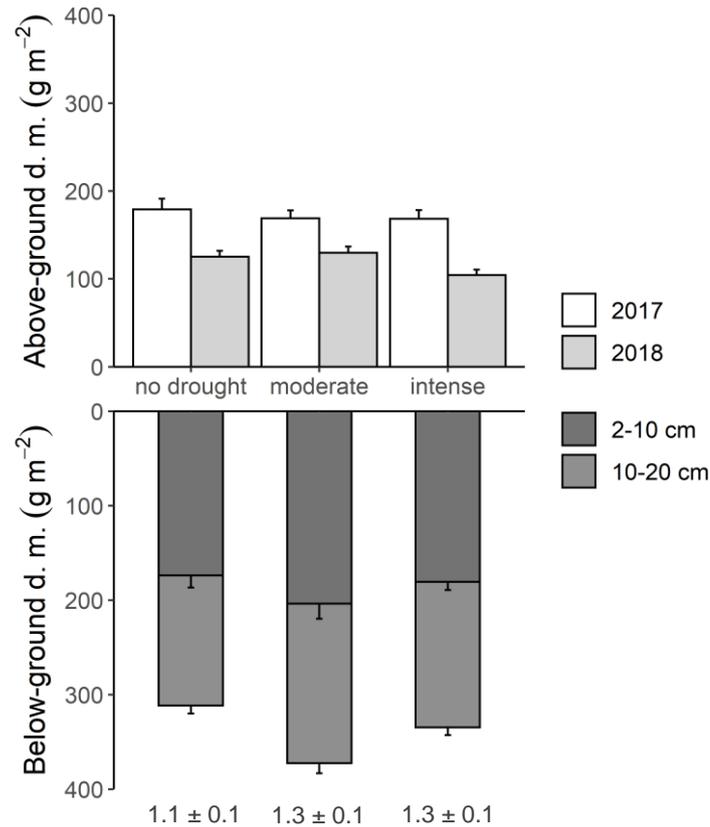
The soil nutrient layer clearly increased the variability in the root mass (Figure 3.6), and therefore, a replicate of three in-growth cores per plot was most likely not enough to find any statistically significant effects of the treatments. It also indicates that the soil nutrient layer was not equally accessed in each in-growth core (in space and time). Treatments, soil depth, and the nutrient layer explained 44% of the variance in root mass.



**Figure 3.5** Root dry mass in g m<sup>-2</sup> (mean + 1 se) after two growing seasons in relation to the drought treatments and snow manipulations, for two soil depths: 2-10 cm and 10-20 cm (volume corrected) of two to three in-growth cores per plot (n = 5)



**Figure 3.6** Effect of an additional nutrient layer (NPK) at 5 cm soil depth on root dry mass in g m<sup>-2</sup> (mean + 1 se) after two growing seasons in relation to the drought treatments and snow manipulations, for two soil depths: 2-10 cm and 10-20 cm (volume corrected) with n = 3



**Figure 3.7** Above-ground phytomass of the growing seasons 2017 and 2018, and below-ground root mass in g m<sup>-2</sup> for soil depths 2-10 cm and 10-20 cm (mean + 1 se) produced across the two growing seasons 2017 and 2018 (n=15, averaged across snow manipulations). Numbers at the bottom indicate the ratio of below- vs. above-ground production (mean ± 1 se)

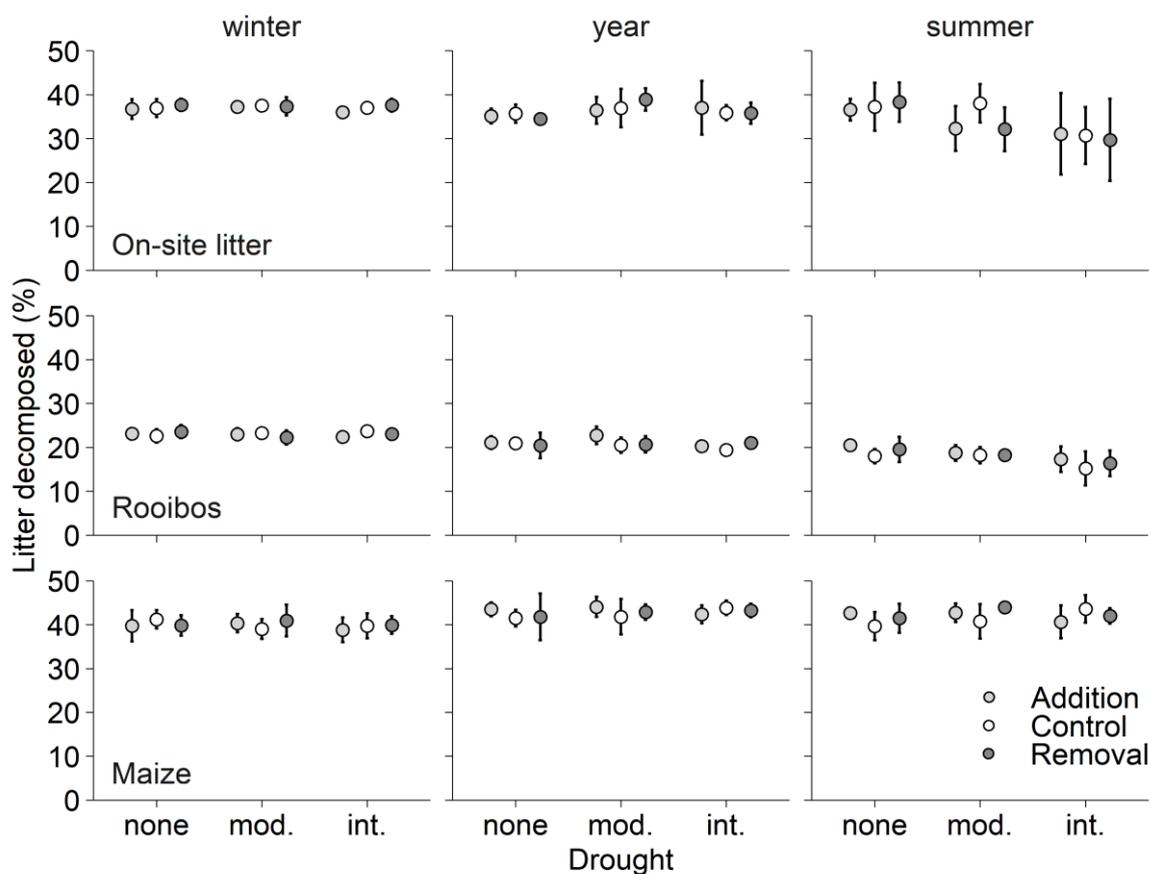
### Above-ground vs. below-ground

We observed contrasting responses of above- and below-ground production to drought, as the above-ground phytomass generally decreased with (intense) drought, and below-ground production increased under moderate drought, but not under intense drought (Figure 3.7). To assess treatment effects on the ratio of below- *versus* above-ground dry matter, we compared the root mass (2-20 cm, growing seasons 2017 and 2018) with the above-ground phytomass formed in 2017 and 2018.

The ratio of above- and below-ground dry matter remained unaffected by snow manipulations ( $p = 0.69$ ), and also drought did not evoke a statistically significant response in the ratio ( $p = 0.21$ ). However, we noticed that under drought, the fraction of root mass increased. On controls, the ratio of below-ground vs. above-ground dry matter was  $1.1 \pm 0.1$ , whereas it was  $1.3 \pm 0.1$  under both moderate and intense drought.

### Litter decomposition

The on-site litter we used for estimating the decomposition had a C:N ratio of 34, indicating a not easily degradable substrate. Over the nine winter months, the litter bags lost  $37.1 \pm 1.5\%$  of their mass, irrespective of snow manipulations ( $p = 0.21$ ) and irrespective of the drought treatment in the previous growing season ( $p = 0.66$ , Figure 3.8). During the subsequent growing season, the yearly series of on-site litter showed no substantial further mass loss, and there was no treatment effect ( $p_{\text{snow}} = 0.91$ ,  $p_{\text{drought}} = 0.18$ ). After exposing a further series of on-site litter bags (same C:N ratio) at the start of the growing season, drought restrained decomposition ( $p = 0.08$ ), as at the end of the growing season there was a  $37.3 \pm 4.1\%$  mass loss on controls, but only  $34.1 \pm 5.3\%$



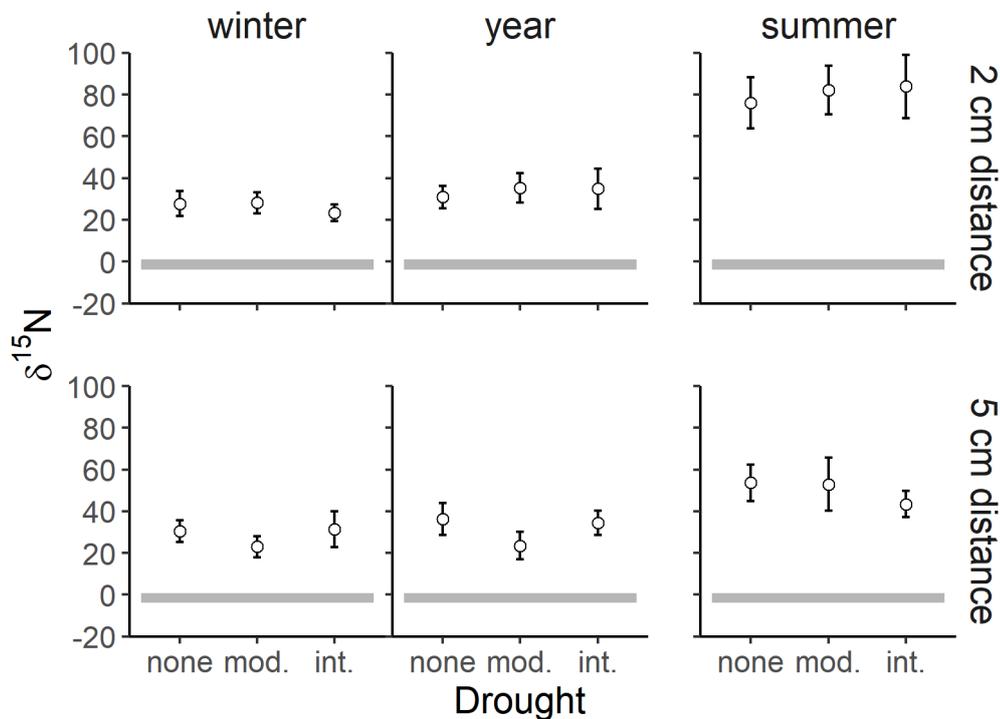
**Figure 3.8** Mass loss in % (mean  $\pm$  sd) of litter bags filled with on-site litter, Rooibos tea and maize leaves, over winter, a whole year, and over summer ( $n = 5$ )

and  $30.5 \pm 7.9\%$  under moderate and intense drought, respectively (2.5 months of exposure). The variability in the mass loss was smallest over winter, whereas it was largest for litter bags that were buried for one growing season only. The variability of the yearly and summer decomposition also increased with the drought treatments. We found no relations between the decomposition rates and the above-ground phytomass or the root mass.

The Rooibos tea with a C:N ratio of 43 (Keuskamp et al. 2013) had an overall smaller mass loss than the on-site litter. Over winter, the mean mass loss was  $23.0 \pm 1.2\%$ , without differences among treatments ( $p_{\text{snow}} = 0.71$ ,  $p_{\text{drought}} = 0.81$ ). As for the on-site litter, the yearly series showed no further mass loss over the subsequent growing season, and also no treatment effects ( $p_{\text{snow}} = 0.22$ ,  $p_{\text{drought}} = 0.22$ ). Tea bags that were brought out at the start of the growing season had lost  $19.4 \pm 2.1\%$  of their weight by the end of the growing season (summer series). There was no significant reduction in mass loss due to moderate drought ( $18.4 \pm 1.5\%$ ,  $p = 0.50$ ), but compared to the controls, the mass loss was significantly lower after intense drought ( $16.3 \pm 3.1\%$ ,  $p < 0.01$ ). The maize litter with a C:N ratio of 14 showed the largest mass loss of all three litter types, with  $39.8 \pm 2.5\%$  loss over winter,  $42.7 \pm 2.7\%$  over a whole year, and  $41.8 \pm 2.9\%$  over summer. There was no effect of either treatment, snow manipulation ( $p = 0.54$ ) or drought ( $p = 0.74$ ) on the maize litter decomposition. We observed that nearly all maize litter bags had a high number of roots grown into them at time of recollection (not quantified).

### Labelled maize litter and the isotopic signal in *Carex curvula* leaves

Adding dissolved enriched  $^{15}\text{N}$  ammoniumnitrate (98%) to growing maize plants in the greenhouse led to enriched maize litter with a  $\delta^{15}\text{N}$  value of  $369.7 \pm 11.5\text{‰}$ . At our study site, the natural  $\delta^{15}\text{N}$  value of youngest *C. curvula* leaves was  $-1.1 \pm 0.9\text{‰}$ . After the winter mineralisation of the maize litter, we already found the  $^{15}\text{N}$  signal of the maize litter in leaves of *C. curvula* in July 2018. In 2 cm distance of the litter bags, the  $\delta^{15}\text{N}$  value was  $26.5 \pm 19.4\text{‰}$ , and in a distance of 5 cm it was  $28.2 \pm 24.9\text{‰}$ . After a whole year at the end of the growing season, these values increased to  $33.7 \pm 28.5\text{‰}$  (2cm) and  $31.5 \pm 26.6\text{‰}$  (5 cm). As the winter series of litter bags were replaced with the summer series at the beginning of the growing season 2018, the surrounding plants were exposed to the twice amount of  $^{15}\text{N}$  enriched maize litter. Accordingly,  $\delta^{15}\text{N}$  in 2 cm distance even reached  $80.7 \pm 49.6\text{‰}$ . We also observed an increase in 5 cm distance, to  $50.0 \pm 36.9\text{‰}$ . Neither the drought treatments nor snow manipulations affected  $\delta^{15}\text{N}$  in *C. curvula* ( $p_{\text{drought}} = 0.94$ ,  $p_{\text{snow}} = 0.61$ ).



**Figure 3.9**  $\delta^{15}\text{N}$  measured in leaves of *C. curvula* in 2 and in 5 cm distance from litter bags filled with  $^{15}\text{N}$  enriched maize leaves (mean  $\pm$  se,  $n=5$ ). Litter bags were exposed over one winter, a whole year and over summer (same location as in winter). The grey bar indicates the natural range of foliar  $\delta^{15}\text{N}$  of *Carex curvula*

## Discussion

In this study, we explored the combined effect of shifting snowmelt dates and of summer drought on a late-successional, alpine grassland. Surprisingly, these two major environmental impacts mostly acted independently of each other, as we found virtually no interaction effects of the treatments. The litter decomposition and nutrient (N) uptake were remarkably robust against earlier snowmelt and summer drought. Our intense drought treatment on top of an already exceptional dry growing season in 2018 clearly impeded the above-ground biomass formation and the decomposition of not easily degradable litter types with C:N ratios greater than 34.

## Phytomass and biomass

### *Above-ground*

With roughly  $180 \text{ g m}^{-2}$  in 2017 and  $125 \text{ g m}^{-2}$  in 2018, we estimated similar amounts of phytomass as Möhl et al. (2020) did for a *C. curvula* dominated grassland in the same study region ( $150\text{--}200 \text{ g m}^{-2}$  in 2014–2016). However, in the 1990s, Schächli and Körner (1996) assessed  $240 \text{ g m}^{-2}$  phytomass very close to our study location. Similarly in a drought experiment in the same region, Schmid et al. (2011) determined  $232 \text{ g m}^{-2}$  phytomass and also in our pre-assessment (2016) we estimated a phytomass production of  $232 \text{ g m}^{-2}$  (data not shown).

The two years studied were rather particular, with an unusually long growing season in 2017 and a dry summer in 2018. However, both elicited an amplification of our treatments, allowing us to study the effects of snowmelt dates and summer drought in a broader spectrum than with the treatments alone.

One of the main effects of our treatments was the pronounced drop of above-ground phytomass (30%) and biomass production (20%) in response to intense drought of 2018. The observed reductions in biomass were in the range of the 12 to 35% noted by Schmid et al. (2011) in a similar setup, and slightly lower than the roughly 40% assessed by de Boeck et al. (2016) after 2.5 weeks of drought in monoliths with highly restricted rooting volume. In our study, the drop in biomass was particularly drastic when we consider that even without drought treatment, the biomass was already 22% lower than in 2017. The growing season 2017 was clearly longer than in 2018, but the weekly formation rates in 2018 dropped by the same magnitude as the overall above-ground biomass production. Thus, the early snowmelt and the long growing season in 2017 were not responsible for the yearly differences. As already mentioned, the growing season 2018 was very dry. The lower biomass formation rates even on controls were thus a consequence of the natural drought, further aggravated in combination with our intense drought treatment.

Our results indicate that not only the intensity, but also its timing and/or duration were decisive for the above-ground biomass production. Namely, the biomass of plots with moderate drought was unaffected or even increased by 9% in case of *C. curvula*, although the soil was equally dry in both drought treatments during the first half of the growing season, when all rainout shelters were still installed. For forbs, there were no pronounced differences between years, but they showed the largest drop in biomass production in response to the intense drought in 2018 (-25%). For montane grasslands, Gilgen and Buchmann (2009) have previously reported that a 45% reduction of precipitation did not reduce the above-ground biomass of forbs, but of graminoids (mostly *Poaceae*).

Multiple studies have reported that they did not observe an effect in the first year of rain exclusion (e.g. Gilgen and Buchmann 2009; Bloor et al. 2010; montane grasslands). However, reduced biomass production as we observed under intense drought in 2018 may impair the growth in the following growing season, as De Boeck et al. (2018) have described legacy effects of drought for an alpine grassland. These included a continuing lower green cover and reduced biomass in the year after the drought. But legacy effects are currently not well understood, as there is also evidence for stimulated above-ground biomass production after drought in lowland grasslands (Griffin-Nolan et al. 2018; Hahn 2019).

Snow removal, and thus a longer growing season did not increase the biomass at time of harvest (at peak biomass). That longer growing seasons do not translate into a higher biomass production has been observed in previous studies with experimental snow removal in the arctic tundra and alpine snowbed species (Wipf et al. 2006, 2009; Baptist et al. 2010b; Wipf 2010). On the other hand, late snowmelt may set temporal limits for growth and result in reduced biomass (Wipf and

Rixen 2010), especially in snowbeds with their very short growing season. In the present study, the snow addition in 2018 did not affect the overall above-ground biomass production, but it increased the calculated weekly formation rates by 19%. Thus, the same amount of biomass was produced during less time.

In *C. curvula*, snow removal in 2017 decreased the formation rate by 25%, suggesting that time was not a limiting factor for biomass production in this species. The onset of above-ground senescence seemed to be related to the onset of the growing season. Although not statistically significant, this was also evidenced by higher amounts of necromass after snow removal in this species and the reverse effect after snow addition, as previously described by Starr et al. (2000). Because photoperiod is known to play an important role for senescence in alpine plants (Körner 2003; Scholz et al. 2018), we were surprised to find two times higher dry weights of necromass (overall and for *C. curvula*) in 2017 than in the following year. However, it is possible that an extremely early onset of the growing season inhibits a clear peak of biomass. Similarly, de Boeck et al. (2016) did not find such a clear peak.

### *Below-ground*

The root mass produced in the in-growth cores (2-20 cm) over two growing seasons and one winter was 255.1 g m<sup>-2</sup>. In a similar grassland in the same region as our experiment, Schmid (2017) assessed the below-ground root production (0-10 cm) by means of standing below-ground biomass, as well as in-growth cores that were buried for three years. The root mass in the in-growth cores was notably higher than in our experiment, as he derived *yearly* production rates of 251 g m<sup>-2</sup>. The standing below-ground biomass of 822 g m<sup>-2</sup> measured by Schmid (0-10 cm; 2017) was clearly lower than the roughly 1200-1500 g m<sup>-2</sup> found in a shading experiment by Möhl et al. (2020) in the top 5 cm alone (both including rhizomes). These high numbers indicate a turnover time of fine roots of several years (Budge et al. 2011).

Hence, the below-ground response of the root mass somewhat differed from the above-ground phytomass. When Schmid (2017) excluded precipitation for six and twelve weeks, the root mass increased by roughly 50%, but mainly in the top 5 cm of the soil. Interestingly, the response of the root mass in in-growth cores differed from those of the standing below-ground biomass. The root mass also increased in the in-growth cores, but after six weeks of rain exclusion by 3% only, and after 12 weeks by 24%. The drought effect was thus mitigated in in-growth cores, which is surprising given the initial lack of competition in the root free soil columns. Thus, it is likely that we underestimated the (positive) drought effect on the root production in our experiment. We found that in contrast to the above-ground phytomass, the root mass increased by 19% under moderate drought, but was unchanged under intense drought, contrasting the results of Schmid (2017) with higher root mass increases after longer periods of rain exclusion. Root growth of *C. curvula* occurs over the whole growing season, but there have been two clear thrusts reported: one in spring and one in autumn (Mähr and Grabherr 1983). In our experiment, the second peak in root growth must therefore have occurred when soil moisture levels and pF values had started to recover in the moderate drought treatment but were still low in the extreme drought treatment. A higher proportional investment into roots after drought has formerly been described for low- and high elevation plant species (Peterson and Billings 1982; Bell and Sultan 1999; Kahmen et al. 2005; Gilgen and Buchmann 2009). Results regarding the increase or decrease of the absolute below-ground root mass are rather inconclusive, with reports of increased (Kahmen et al. 2005; lowland), decreased (Fiala et al. 2009, lowland - montane) or unchanged (Gilgen and Buchmann 2009; Fuchslueger et al. 2014; montane and subalpine) below-ground root mass, mostly

measured in in-growth cores. Reasons may be different drought intensities (Vicca et al. 2012; Knapp et al. 2017), as also demonstrated by the contrasting response of root growth to the two drought treatments in our experiment, but also through differences in root mortalities (we found no senesced roots after two growing seasons). Moreover, it is of crucial importance to report the soil texture and pF values (matrix potential), that substantially affect the outcome of drought experiments, as it affects the quantity of plant-available water in the soil that may differ drastically between experiments (Weng and Luo 2008).

We were surprised to find an equal ratio of above- and below-ground dry matter under both drought treatments, as we would have expected larger proportional investments into roots after more severe drought conditions. However, the intense drought treatment clearly impeded the overall biomass production, with large above-ground reductions. In line with increased investments into storage organs under drought (Schmid 2017), Hasibeder et al. (2015) showed that eight weeks of rain exclusion in a subalpine grassland significantly enhanced the storage of fresh assimilates in below-ground organs, while the overall C uptake of the grassland and the root respiration were reduced ( $^{13}\text{C}$  pulse labelling experiment in a subalpine meadow). Biomass allocation patterns do not necessarily reflect in the concentration of non-structural carbohydrates of below-ground organs, as Möhl et al. (2020) found that shade reduced the amount of rhizomes without affecting their concentration of non-structural carbohydrates.

## **Decomposition and nutrient accessibility**

### *Decomposition*

Over the nine winter months, the on-site litter bags showed a substantial mass loss of 37% already, with no further decline during the following growing season. Baptist et al. (2010a), who exposed litter in the French Alps for 1.5 years, also observed the highest mass loss after the first winter. Such high winter decomposition is in line with a significant C release over the snow covered winter months (Brooks et al. 1996; Fahnestock et al. 1998, 1999). For an alpine grassland, Scholz et al. (2018) measured winter fluxes of  $0.3 \text{ g C m}^{-2} \text{ d}^{-1}$  by means of an eddy tower, with a total winter release of  $90 \text{ g C m}^{-2}$ . The efflux rates decreased over winter, presumably due to a decrease in substrate availability for microbes. Apart from leaching of water soluble litter substances (Seastedt et al. 2001; Gavazov 2010), this winter decomposition is most likely accomplished by a microbial community dominated by fungi. After snowmelt, the total microbial biomass decreases (Lipson et al. 2000), and there is a shift towards bacterially-dominated communities (Schadt et al. 2003; Björk et al. 2008; Zinger et al. 2009). This goes along with an alteration in substrates, with plant litter in autumn and winter, and living roots and exudates in summer (Lipson et al. 2002). A pulse-labelling experiment with  $^{13}\text{CO}_2$  revealed that the transfer of C from plants to fungi was uninterrupted by drought, in contrast to the transfer to bacteria. Moreover, the relative abundance of Gram-negative bacteria benefiting from root exudates decreased, whereas the abundance of generally more drought-resistant Gram-positive bacteria increased (Fuchslueger et al. 2014). When we buried a series of on-site litter bags at the start of the growing season for 2.5 months, we observed a similar amount of decomposition as over the longer winter (9 months). Thus, litter would be decomposed if it was available at the start of the growing season.

In contrast to the results of Baptist et al. (2010a), we did not find any further decomposition of litter (yearly series) during the subsequent growing season. Litter mass loss usually follows an exponential decline (see Figure 2 in Keuskamp et al. 2013). It is thus very likely that all the easily decomposable elements were already decomposed over winter. Litter quality has been reported to have a large effect on decomposition (Nadelhoffer et al. 1991; Hobbie 1996; Arnone and Hirschel

1997; Baptist et al. 2010a). Maize litter with a very low C:N ratio of 14 was thus decomposed much faster than the on-site litter and Rooibos tea with C:N ratios of 34 and 43. Nevertheless, the mass loss of these two litter types was surprisingly high given the rule of thumb established in agriculture that states that mineralisation occurs at C:N ratios below roughly 25 (Blume et al. 2016). We found that on-site litter and Rooibos tea brought out at the start of the growing season decomposed more slowly under drought. It is likely that we would have found a similar effect for the maize litter earlier in the season. Potentially, we would have observed less mass loss and a slightly more pronounced drought effect if we would have used senesced on-site litter exclusively. However, Lambie et al. (2014) showed that at least under laboratory conditions the stage of litter senescence has no effect on the CO<sub>2</sub> production of microbes. Hättenschwiler and Gasser (2005) demonstrated that the decomposition of low-quality litter of deciduous forests was enhanced when mixed with easier decomposable litter of other tree species. In their review Hättenschwiler et al. (2005) highlighted how litter types affect the decomposer community and thus, the soil fauna is highly adapted to the local plant community. However, the presence of functional decomposer groups seems to be more relevant for the decomposition than the abundance of single species.

#### *Nutrient uptake and root foraging*

One of our main hypotheses was that drought would not heavily affect the alpine species of the late successional grassland through direct desiccation and turgor loss, but through limited nutrient accessibility. However, our labelling experiment with maize litter enriched in <sup>15</sup>N highlighted two aspects (1): at least the mesofauna responsible for the first steps of the decomposition, as well as the microorganisms were not impaired by our experimental treatments (macrofauna was excluded by litter bag mesh), and (2) the nutrient uptake in the dominant sedge remained intact. Alpine graminoids are able to profit from pulsed nutrient inputs (Bowman and Bilbrough 2001; Körner 2003) and thus, the N mineralised over winter was quickly taken up by *C. curvula*. That the foliar signal of <sup>15</sup>N in *C. curvula* further increased over the summer underpins that the N uptake continued over the growing season.

Although the mineralisation of on-site litter was slowed down under intense drought, the maize litter was still mineralised and assimilated by *C. curvula* under these dry conditions. The second exposure to labelled maize led to a 30% stronger enrichment in foliar  $\delta^{15}\text{N}$  values in a 2 cm than in a 5 cm distance from the litter bags. The lateral dispersion of the mineralised N was therefore smaller during the growing season, which is surprising given the high density of *C. curvula* roots and vegetative shoot growth rates in the range of 0.4 mm a<sup>-1</sup> (Erschbamer et al. 1994; De Witte et al. 2012). It is possible that root exudates facilitated the contact between roots and soil during the desiccation of the soil (Walker et al. 2003), ultimately sustaining the nutrient uptake.

That we noticed (but remained unquantified) a high number of roots growing directly around and into the maize litter bags underlines the foraging for nutrients as described in Körner (2003). In accordance with these observations, we also found 77.7% more root mass after providing an additional nutrient layer (NPK) within the in-growth cores. But in contrast to the foliar  $\delta^{15}\text{N}$  in *C. curvula*, the nutrient layer combined with drought did not lead to such a boost in the root growth (plus 12.9% under moderate drought only). Under intense drought, there was no significant increase in root mass due to the nutrient layer. This was in contrast to the high number of roots we had observed growing around the maize litter bags. A heterogeneous distribution of plant litter in the soil and the presence of microorganisms both increase the foraging root growth (Bonkowski

et al. 2000; Bonkowski 2004; shown for *Lolium perenne*). Possibly, the activity of the mesofauna and microorganisms in and around the maize litter bags was higher than in the ingrowth cores filled with root free soil. Thus, the foraging root growth may have been promoted more strongly around the litter bags with high mineralisation rates. It is further possible that the often nutrient limited microbes (Niklaus and Körner 1996) immobilised a large part of the easily available nutrient layer before newly formed roots gained access to it, and this access was slower under drought. Moreover, the additional nutrients were offered as thin layer at a soil depth of 5 cm, where the root density generally starts to decrease, whereas the maize litter bags were placed 0 to 7 cm beneath the surface. Overall, the understanding of root foraging is still rather limited, and Mommer et al. (2012) showed that *Agrostis stolonifera* produced more roots in nutrient rich patches, but avoided them under interspecific competition with *Rumex palustris*.

## Conclusions

The studied late successional grassland dominated by *C. curvula* was surprisingly robust against shifting snowmelt dates and summer drought. So far, we found no evidence that shifting snowmelt dates and an earlier onset of the growing season amplifies the consequences of summer droughts. Summer droughts that do not span over the whole growing season shifts biomass allocation more into below-ground plant organs.

Extreme droughts as observed in 2018 or worse, with the additional rain exclusion during more than ten weeks, severely reduced the above-ground phytomass of all functional groups. However, forbs were more affected than the dominant sedge *C. curvula*, which may lead to a shift in the species composition in the longer term.

The substantial fraction of the litter decomposition occurred over the winter. The N uptake of mineralisation products by plants was unimpeded by rain exclusion that spanned almost an entire growing season. However, below-ground foraging for punctual nutrient sources may be impaired in years with extreme drought.

## References

- Addington RN, Seastedt TR (1999) Activity of soil microarthropods beneath snowpack in alpine tundra and subalpine forest. *Pedobiologia (Jena)* 43:47–53
- Arnone JA, Hirschel G (1997) Does fertilizer application alter the effects of elevated CO<sub>2</sub> on *Carex* leaf litter quality and in situ decomposition in an alpine grassland? *Acta Oecologica* 18:201–206. doi: 10.1016/S1146-609X(97)80006-9
- Baptist F, Flahaut C, Streb P, Choler P (2010a) No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. *Plant Biol* 12:755–764. doi: 10.1111/j.1438-8677.2009.00286.x
- Baptist F, Yoccoz NG, Choler P (2010b) Direct and indirect control by snow cover over decomposition in alpine tundra along a snowmelt gradient. *Plant Soil* 328:397–410. doi: 10.1007/s11104-009-0119-6
- Bassin S, Schalajda J, Vogel A, Suter M (2012) Different types of sub-alpine grassland respond similarly to elevated nitrogen deposition in terms of productivity and sedge abundance. *J Veg Sci* 23:1024–1034. doi: 10.1111/j.1654-1103.2012.01422.x
- Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Scheipl F, Grothendieck G, Green P, Fox J (2020) R package lme4: Linear mixed-effects models using «Eigen» and S4. p 124
- Bell DL, Sultan SE (1999) Dynamic phenotypic plasticity for root growth in *Polygonum*: A comparative study. *Am J Bot* 86:807–819. doi: 10.2307/2656702

- Björk RG, Björkman MP, Andersson MX, Klemedtsson L (2008) Temporal variation in soil microbial communities in Alpine tundra. *Soil Biol Biochem* 40:266–268. doi: 10.1016/j.soilbio.2007.07.017
- Bloor JMG, Pichon P, Falcimagne R, Leadley P, Soussana J-F (2010) Effects of warming, summer drought, and CO<sub>2</sub> enrichment on aboveground biomass production, flowering phenology, and community structure in an upland grassland ecosystem. *Ecosystems* 13:888–900. doi: 10.1007/s10021-010-9363-0
- Blume-Werry G, Jansson R, Milbau A (2017) Root phenology unresponsive to earlier snowmelt despite advanced above-ground phenology in two subarctic plant communities. *Funct Ecol* 31:1493–1502. doi: 10.1111/1365-2435.12853
- Blume H-P, Brümmer GW, Fleige H, Horn R, Kandeler E, Kögel-Knabner I, Kretzschmar R, Stahr K, Wilke B-M (2016) Scheffer/Schachtschabel Soil science, 16<sup>th</sup> edn. Springer, Berlin Heidelberg, p 618
- Bonkowski M (2003) Protozoa and plant growth: The microbial loop in soil revisited. *New Phytol* 162:617–631. doi: 10.1111/j.1469-8137.2004.01066.x
- Bonkowski M, Griffiths B, Scrimgeour C (2000) Substrate heterogeneity and microfauna in soil organic «hotspots» as determinants of nitrogen capture and growth of ryegrass. *Appl Soil Ecol* 14:37–53. doi: 10.1016/S0929-1393(99)00047-5
- Bowman WD, Billbrough CJ (2001) Influence of a pulsed nitrogen supply on growth and nitrogen uptake in alpine graminoids. *Plant Soil* 233:283–290. doi: 10.1023/A:1010571920890
- Brooks PD, Williams MW (1999) Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrol Process* 13:2177–2190
- Brooks PD, Williams MW, Schmidt SK (1996) Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry* 32:93–113. doi: 10.1007/BF00000354
- Brooks PD, Williams MW, Schmidt SK (1998) Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. *Biogeochemistry* 43:1–15
- Budge K, Leifeld J, Hiltbrunner E, Fuhrer J (2011) Alpine grassland soils contain large proportion of labile carbon but indicate long turnover times. *Biogeosciences* 8:1911–1923. doi: 10.5194/bg-8-1911-2011
- Calanca P (2007) Climate change and drought occurrence in the Alpine region: How severe are becoming the extremes? *Glob Planet Change* 57:151–160. doi: 10.1016/j.gloplacha.2006.11.001
- Ceppi P, Scherrer SC, Fischer AM, Appenzeller C (2012) Revisiting Swiss temperature trends 1959–2008. *Int J Climatol* 32:203–213. doi: 10.1002/joc.2260
- Cornelius C, Leingärtner A, Hoiss B, Menzel A (2013) Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. *J Exp Bot* 64:241–251. doi: 10.1093/jxb/err313
- de Boeck HJ, Bassin S, Verlinden M, Zeiter M, Hiltbrunner E (2016) Simulated heat waves affected alpine grassland only in combination with drought. *New Phytol* 209:531–541. doi: 10.1111/nph.13601
- De Boeck HJ, Hiltbrunner E, Verlinden M, Bassin S, Zeiter M (2018) Legacy effects of climate extremes in alpine grassland. *Front Plant Sci* 871:1–10. doi: 10.3389/fpls.2018.01586
- De Witte LC, Armbruster GFJ, Gielly L, Taberlet P, Stöcklin J (2012) AFLP markers reveal high clonal diversity and extreme longevity in four key arctic-alpine species. *Mol Ecol* 21:1081–1097. doi: 10.1111/j.1365-294X.2011.05326.x
- Erschbamer B, Winkler J, Wagner J (1994) The vegetative and generative development of three *Carex curvula* in the Central Alps. *Flora* 189:277–286
- Fahnestock JT, Jones MH, Brooks PD, Walker DA, Welker JM (1998) Winter and early spring CO<sub>2</sub> efflux from tundra communities of northern Alaska. *J Geophys Res* 103:29,023–29,027. doi: 10.1097/RHU.0b013e318177627d.Interferon
- Fahnestock JT, Jones MH, Welker JM (1999) Wintertime CO<sub>2</sub> efflux from arctic soils: implications for annual carbon budgets. *Global Biogeochem Cycles* 13:775–779
- Fiala K, Tůma I, Holub P (2009) Effect of manipulated rainfall on root production and plant belowground dry mass of different grassland ecosystems. *Ecosystems* 12:906–914. doi: 10.1007/s10021-009-9264-2
- Frankenberger WT, Abdelmagid HM (1985) Kinetic parameters of nitrogen mineralization rates of leguminous crops incorporated into soil I. *Plant Soil* 87:257–271

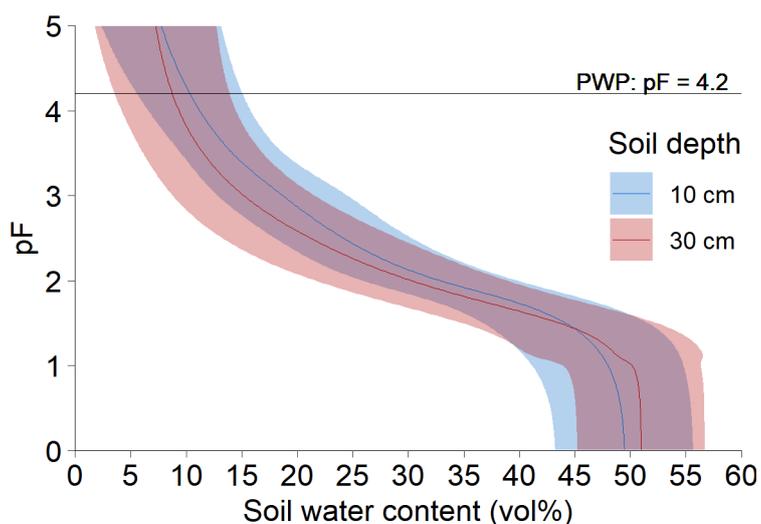
- Freschet T, Cornelissen JHC, Van Logtestijn RSP, Aerts R (2010) Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? *New Phytol* 186:879–889. doi: 10.1111/j.1469-8137.2010.03228.x
- Fuchslueger L, Bahn M, Fritz K, Hasibeder R, Richter A (2014) Experimental drought reduces the transfer of recently fixed plant carbon to soil microbes and alters the bacterial community composition in a mountain meadow. *New Phytol* 201:916–927. doi: 10.1111/nph.12569
- Gavazov KS (2010) Dynamics of alpine plant litter decomposition in a changing climate. *Plant Soil* 337:19–32. doi: 10.1007/s11104-010-0477-0
- Gerzabek MH, Haberhauer G, Stemmer M, Klepsch S, Haunold E (2004) Long-term behaviour of  $^{15}\text{N}$  in an alpine grassland ecosystem. *Biogeochemistry* 70:59–69. doi: 10.1023/B: BIOG.0000049336.84556.62
- Gilgen AK, Buchmann N (2009) Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. *Biogeosciences* 6:2525–2539. doi: 10.5194/bg-6-2525-2009
- Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J, Stoffel M (2014) 21<sup>st</sup> century climate change in the European Alps - A review. *Sci Total Environ* 493:1138–1151. doi: 10.1016/j.scitotenv.2013.07.050
- Grabherr G (1987) Produktion und Produktionsstrategien im Kurmmseggenrasen (*Caricetum curvulae*) der Silikatalpen und ihre Bedeutung für die Bestandesstruktur. In: MaB-Projekt Obergurgl. Patzelt, Gernot, Innsbruck, pp 233–242
- Griffin-Nolan RJ, Carroll CJW, Denton EM, Johnston MK, Collins SL, Smith MD, Knapp AK (2018) Legacy effects of a regional drought on aboveground net primary production in six central US grasslands. *Plant Ecol* 219:505–515. doi: 10.1007/s11258-018-0813-7
- Hahn C (2019) Seasonal effects of drought on the productivity and fodder quality of temperate grassland species. Dissertation. University of Basel. p 129
- Hasibeder R, Fuchslueger L, Richter A, Bahn M (2015) Summer drought alters carbon allocation to roots and root respiration in mountain grassland. *New Phytol* 205:1117–1127. doi: 10.1111/nph.13146
- Hättenschwiler S, Gasser P (2005) Soil animals alter plant litter diversity effects. *PNAS* 102:1519–1524. doi: 10.1073/pnas.0404977102
- Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annu Rev Ecol Evol Syst* 36:191–218. doi: 10.1146/annurev.ecolsys.36.112904.151932
- Hiltbrunner E, Schwikowski M, Körner C (2005) Inorganic nitrogen storage in alpine snow pack in the Central Alps (Switzerland). *Atmos Environ* 39:2249–2259. doi: 10.1016/j.atmosenv.2004.12.037
- Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol Monogr* 66:503–522
- Hobbie SE, Chapin FS (1996) Winter regulation of tundra litter carbon and nitrogen dynamics. *Biogeochemistry* 35:327–338. doi: 10.1007/BF02179958
- Hock R, Rasul G, Adler C, Cáceres B, Gruber S, Hirabayashi Y, Jachson M, Kääb A, Kang S, Kutuzov S, Milner A, Molau U, Morin S, Orlove B, Steltzer H (2019) High mountain areas. In: Pörtner H-O, Roberts DC, Masson-Delmotte V, et al. (eds) IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. In press. p 202
- Hülber K, Gottfried M, Pauli H, Reiter K, Winkler M, Grabherr G (2006) Phenological responses of snowbed species to snow removal dates in the central Alps: Implications for climate warming. *Arctic, Antarct Alp Res* 38:99–103. doi: 10.1657/1523-0430(2006)038[0099:PROSST]2.0.CO;2
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362. doi: 10.1890/06-2128.1
- IPCC (2018) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner H, et al. (eds) *Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change*. Geneva, Switzerland, pp 374–381
- Isard SA (1986) Factors influencing soil moisture and plant community distributions on Niwot Ridge, Front Range, Colorado, USA. *Arct Alp Res* 18:83–96. doi: 10.2307/1551216
- Jaeger CH, Monson RK, Fisk MC, Schmidt SK (1999) Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem. *Ecology* 80:1883–1891

- John A, Weisberg S, Price B, Adler D, Bates D, Baud-bovy G, Bolker B, Ellison S, Graves S, Krivitsky P, Laboissiere R, Maechler M, Monette G, Murdoch D, Ogle D, Ripley B, Venables W, Walker S, Winsemius D (2020) R package car: Companion to applied regression. p 150
- Jonasson S, Havström M, Jensen M, Callaghan TV (1993) In situ mineralization of nitrogen and phosphorus of arctic soils after perturbations simulating climate change. *Oecologia* 95:179–186. doi: 10.1007/BF00323488
- Jonasson S, Michelsen A, Schmidt IK, Nielsen E V., Callaghan T V. (1996) Microbial biomass C, N and P in two arctic soils and responses to addition of NPK fertilizer and sugar: Implications for plant nutrient uptake. *Oecologia* 106:507–515. doi: 10.1007/BF00329709
- Jonasson S, Michelsen A, Schmidt IK, Nielsen E V. (1999) Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. *Ecology* 80:1828–1843. doi: 10.1890/0012-9658(1999)080[1828:RIMAPT]2.0.CO;2
- Kahmen A, Perner J, Buchmann N (2005) Diversity-dependent productivity in semi-natural grasslands following climate perturbations. *Funct Ecol* 19:594–601. doi: 10.1111/j.1365
- Keller F, Körner C (2003) The role of photoperiodism in alpine plant development. *Arctic, Antarct Alp Res* 35:361–368. doi: 10.1657/1523-0430(2003)035[0361:TROPIA]2.0.CO;2
- Keuskamp JA, Dingemans BJJ, Lehtinen T, Sarneel JM, Hefting MM (2013) Tea Bag Index: A novel approach to collect uniform decomposition data across ecosystems. *Methods Ecol Evol* 4:1070–1075. doi: 10.1111/2041-210X.12097
- Knapp AK, Avolio ML, Beier C, Carroll CJW, Collins SL, Dukes JS, Fraser LH, Griffin-Nolan RJ, Hoover DL, Jentsch A, Loik ME, Phillips RP, Post AK, Sala OE, Slette IJ, Yahdjian L, Smith MD (2017) Pushing precipitation to the extremes in distributed experiments: recommendations for simulating wet and dry years. *Glob Chang Biol* 23:1774–1782. doi: 10.1111/gcb.13504
- Körner C (2003) Alpine plant life. Functional plant ecology of high mountain ecosystems, 2<sup>nd</sup> edn. Springer, Berlin Heidelberg. p 349
- Körner C (2014) Ökologie. In: Kadereit JW, Körner C, Kost B, Sonnewald U (eds) Strasburger Lehrbuch der Pflanzenwissenschaften. Springer, Berlin Heidelberg, pp 740–810
- Kosonen Z, Schnyder E, Hiltbrunner E, Thimonier A, Schmitt M, Seitler E, Thöni L (2019) Current atmospheric nitrogen deposition still exceeds critical loads for sensitive, semi-natural ecosystems in Switzerland. *Atmos Environ* 211:214–225. doi: 10.1016/j.atmosenv.2019.05.005
- Lenth R, Henrik S, Love J, Buerkner P, Herve M (2019) R package emmeans: Estimated marginal means, aka least-squares means. p 81
- Lipson D, Näsholm T (2001) The unexpected versatility of plants: Organic nitrogen use and availability in terrestrial ecosystems. *Oecologia* 128:305–316. doi: 10.1007/s004420100693
- Lipson DA, Schadt CW, Schmidt SK (2002) Changes in soil microbial community structure and function in an alpine dry meadow following spring snow melt. *Microb Ecol* 43:307–314. doi: 10.1007/s00248-001-1057-x
- Lipson DA, Schmidt SK, Monson RK (1999) Links between microbial population dynamics and nitrogen availability in an alpine ecosystem. *Ecology* 80:1623–1631
- Lipson DA, Schmidt SK, Monson RK (2000) Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. *Soil Biol Biochem* 32:441–448. doi: 10.1016/S0038-0717(99)00068-1
- Mähr E, Grabherr G (1983) Wurzelwachstum und -produktion in einem Krummseggenrasen (*Caricetum curvulae*) der Hochalpen. In: Bohm W, Kutschera L, Lichtenegger E (eds) Wurzelökologie und ihre Nutzenanwendung. Ein Beitrag zur Erforschung der Gesamtpflanze. Int Symp 27-39 Sept 1982. Bundesanstalt für alpenländische Landwirtschaft, Irnding, pp 405–416
- Miller AE, Bowman WD (2003) Alpine plants show species-level differences in the uptake of organic and inorganic nitrogen. *Plant Soil* 250:283–292. doi: 10.1023/A:1022867103109
- Möhl P, Hiltbrunner E, Körner C (2020) Halving sunlight reveals no carbon limitation of above-ground biomass production in alpine grassland. *Glob Chang Biol* 26:1857–1872. doi: 10.1111/gcb.14949
- Mommer L, van Ruijven J, Jansen C, van de Steeg HM, de Kroon H (2012) Interactive effects of nutrient heterogeneity and competition: Implications for root foraging theory? *Funct Ecol* 26:66–73. doi: 10.1111/j.1365-2435.2011.01916.x
- Moorhead DL, Reynolds JF (1993) Effects of climate change on decomposition in Arctic tussock tundra: A modeling synthesis. *Arct Alp Res* 25:403–412. doi: 10.2307/1551923

- Nadelhoffer KJ, Giblin AE, Shaver GR, Laundre JA (1991) Effects of temperature and substrate quality on element mineralization in six Arctic soils. *Ecology* 72:242–253
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142. doi: 10.1111/j.2041-210x.2012.00261.x
- NCCS (2018) CH2018 – Klimaszenarien für die Schweiz. <https://www.nccs.admin.ch/nccs/de/home/materialien-und-daten/daten/ch2018-webatlas.html>. Accessed 25 Jun 2020
- Niklaus PA, Körner C (1996) Responses of soil microbiota of a late successional alpine grassland to long term  $\text{CO}_2$  enrichment. *Plant Soil* 184:219–229. doi: 10.1007/BF00010451
- O’Lear HA, Seastedt TR (1994) Landscape patterns of litter decomposition in alpine tundra. *Oecologia* 99:95–101. doi: 10.1007/BF00317088
- Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:322–331
- Peterson KM, Billings WD (1982) Growth of alpine plants under controlled drought. *Arct Alp Res* 14:189–194. doi: 10.2307/1551151
- R Core Team (2019) R: A language and environment for statistical computing
- Rajczak J, Pall P, Schär C (2013) Projections of extreme precipitation events in regional climate simulations for Europe and the Alpine region. *J Geophys Res Atmos* 118:3610–3626. doi: 10.1002/jgrd.50297
- Rebetez M, Reinhard M (2008) Monthly air temperature trends in Switzerland 1901–2000 and 1975–2004. *Theor Appl Climatol* 91:27–34. doi: 10.1007/s00704-007-0296-2
- Sanaullah M, Rumpel C, Charrier X, Chabbi A (2012) How does drought stress influence the decomposition of plant litter with contrasting quality in a grassland ecosystem? *Plant Soil* 352:277–288. doi: 10.1007/s11104-011-0995-4
- Schadt CW, Martin AP, Lipson DA, Schmidt SK (2003) Seasonal dynamics of previously unknown fungal lineages in tundra soils. *Science* 301:1359–1361. doi: 10.1126/science.1086940
- Schäppi B, Körner C (1996) Growth responses of an alpine grassland to elevated  $\text{CO}_2$ . *Oecologia* 105:43–52
- Schäppi B, Körner CH (1997) In situ effects of elevated  $\text{CO}_2$  on the carbon and nitrogen status of alpine plants. *Funct Ecol* 11:290–299
- Schimmel JP, Bilbrough C, Welker JM (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two arctic tundra communities. *Soil Biol Biochem* 36:217–227. doi: 10.1111/jsap.12063
- Schmid S (2017) Impacts of climate change on alpine grassland ecosystems: Responses in structure and function. Dissertation. ETH Zürich. p 170
- Schmid S, Hiltbrunner E, Spehn E, Lüscher A, Scherer-Lorenzen M (2011) Impact of experimentally induced summer drought on biomass production in alpine grassland. *Grassl Sci Eur* 16:214–216
- Scholz K, Hammerle A, Hiltbrunner E, Wohlfahrt G (2018) Analyzing the effects of growing season length on the net ecosystem production of an alpine grassland using model–data fusion. *Ecosystems* 21:982–999. doi: 10.1007/s10021-017-0201-5
- Seastedt TR, Walker MD, Bryant DM (2001) Controls on decomposition processes in alpine tundra. In: Bowman WD, Seastedt TR (eds) *Structure and function of an alpine ecosystem - Niwot Ridge, Colorado*. Oxford University Press, pp 222–235
- Starr G, Oberbauer SF, Pop EW (2000) Effects of lengthened growing season and soil warming on the phenology and physiology of *Polygonum bistorta*. *Glob Chang Biol* 6:357–369. doi: 10.1046/j.1365-2486.2000.00316.x
- Steinger T, Körner C, Schmid B (1996) Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. *Oecologia* 105:94–99
- Vicca S, Gilgen AK, Camino Serrano M, Dreesen FE, Dukes JS, Estiarte M, Gray SB, Guidolotti G, Hoepfner SS, Leakey ADB, Ogaya R, Ort DR, Ostrogovic MZ, Rambal S, Sardans J, Schmitt M, Siebers M, van der Linden L, van Straaten O, Granier A (2012) Urgent need for a common metric to make precipitation manipulation experiments comparable. *New Phytol* 195:518–522. doi: 10.1111/j.1469-8137.2012.04224.x
- Walker TS, Bais HP, Grotewold E, Vivanco JM (2003) Root exudation and rhizosphere biology. *Plant Physiol* 132:44–51. doi: 10.1104/pp.102.019661

- Weng E, Luo Y (2008) Soil hydrological properties regulate grassland ecosystem responses to multifactor global change: A modeling analysis. *J Geophys Res Biogeosciences* 113:1–16. doi: 10.1029/2007JG000539
- Wipf S (2010) Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecol* 207:53–66. doi: 10.1007/sl
- Wipf S, Rixen C (2010) A review of snow manipulation experiments in arctic and alpine tundra ecosystems. *Polar Res* 29:95–109. doi: 10.1111/j.1751-8369.2010.00153.x
- Wipf S, Rixen C, Mulder CPH (2006) Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Glob Chang Biol* 12:1496–1506. doi: 10.1111/j.1365-2486.2006.01185.x
- Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Clim Change* 94:105–121. doi: 10.1007/s10584-009-9546-x
- Zinger L, Shahnavaz B, Baptist F, Geremia RA, Choler P (2009) Microbial diversity in alpine tundra soils correlates with snow cover dynamics. 850–859. doi: 10.1038/ismej.2009.20

### Supplemental material for chapter 3



**Figure S3.1** pF curve (mean ± sd), derived from 8 and 7 single pF curves for 10 cm and 30 cm soil depth, respectively. PWP is the permanent wilting point

**Table S3.1** The root mass (mean ± sd, in g m<sup>-2</sup>) of in-growth cores over two growing seasons (2017-2018), for the two soil depths 2-10 cm and 10-20 cm, without (top, n = 5) or without (bottom, n = 3) nutrient layer (NPK)

Root mass		Total	2-10 cm	10-20 cm
none	add	270.5 ± 51.0	174.8 ± 47.7	95.7 ± 10.1
	cont	273.1 ± 83.4	164.9 ± 64.5	108.2 ± 21.6
	rem	308.8 ± 77.7	182.0 ± 45.7	126.8 ± 35.2
mod	add	355.3 ± 132.6	210.4 ± 92.2	144.9 ± 41.6
	cont	348.0 ± 87.3	218.6 ± 58.8	129.4 ± 35.5
	rem	313.2 ± 40.4	182.1 ± 23.8	131.0 ± 25.0
int	add	317.8 ± 64.8	186.2 ± 36.0	131.6 ± 31.5
	cont	315.1 ± 43.7	196.9 ± 23.8	118.2 ± 22.7
	rem	278.7 ± 56.1	159.0 ± 32.5	119.7 ± 25.5

Root mass		2-10 cm		10-20 cm	
NPK		no NPK	NPK	no NPK	NPK
none	add	159.7 ± 6.1	216.8 ± 102.8	92.1 ± 12.3	114.4 ± 29.7
	cont	132.3 ± 22.1	235.2 ± 170.2	94.3 ± 9.1	112.7 ± 40.9
	rem	184.7 ± 59.0	270.9 ± 68.8	121.8 ± 48.7	137.6 ± 9.0
mod	add	173.5 ± 31.7	192.5 ± 40.4	132.4 ± 28.2	107.5 ± 27.9
	cont	206.7 ± 70.5	233.4 ± 60.9	129.6 ± 49.8	112.7 ± 12.5
	rem	178.0 ± 20.6	245.4 ± 91.3	116.8 ± 22.2	141.1 ± 35.5
int	add	180.3 ± 33.9	199.9 ± 64.2	124.6 ± 12.3	123.6 ± 46.1
	cont	190.8 ± 30.1	181.1 ± 49.9	106.3 ± 15.5	119.2 ± 24.0
	rem	138.5 ± 22.1	200.8 ± 20.1	101.1 ± 2.6	139.5 ± 35.9

**Table S3.2** Test statistics  $X^2(df)$  p-value (ANOVA) for the phytomass, biomass, necromass, weekly biomass formation, and root mass, with the effects of years, drought treatment, snow manipulation, and the interaction of drought treatments and snow manipulations (S x D). The test statistics ( $X^2$  (df) p-value) are assessed from models with stepwise backwards model selection. The effect of the year stems from a model which includes all interaction effects of years and treatments in its full form (year x drought x snow manipulation) as we found no interaction of treatments and years. The treatment effects were assessed for the two years individually.

	Year	2017				2018			
		Drought	Snow man	S x D	Drought	Snow man	S x D		
Phytomass	61.8(1) <0.01	0.6(2) 0.73	0.7(2) 0.72	1.5(4) 0.83	9.7(2) 0.01	2.1(2) 0.35	1.1(4) 0.90		
Sedge	35.0(1) <0.01	1.8(2) 0.41	2.8(2) 0.24	1.5(4) 0.82	0.1(2) 0.95	0.7(2) 0.04	1.8(4) 0.76		
Graminoids	28.2(1) <0.01	2.9(2) 0.24	2.2(2) 0.34	3.8(4) 0.43	2.2(2) 0.34	0.5(2) 0.79	9.7(4) 0.05		
Forbs	8.7(1) <0.01	2.3(2) 0.32	0.6(2) 0.75	7.2(4) 0.13	7.0(2) 0.03	2.0(2) 0.36	1.9(4) 0.76		
Necromass	15.4(1) <0.01	2.0(2) 0.38	6.7(2) 0.04	1.9(4) 0.76	1.4(2) 0.50	9.0(2) 0.01	4.3(4) 0.37		
Sedge	46.3(1) <0.01	0.5(2) 0.79	4.6(2) 0.11	7.2(4) 0.13	1.9(2) 0.39	8.1(2) 0.02	5.8(4) 0.21		
Graminoids	110.9(1) <0.01	3.8(1) <0.01	0.4(2) 0.82	4.2(4) 0.38	5.1(2) 0.08	0.6(2) 0.72	6.6(4) 0.16		
Forbs	123.1(1) <0.01	3.6(2) 0.16	2.8(2) 0.25	2.0(4) 0.73	2.3(2) 0.31	0.2(2) 0.90	3.7(4) 0.44		
Biomass	29.4(1) <0.01	0.38(2) 0.83	0.19(2) 0.91	2.9(4) 0.58	10.9(2) <0.01	2.2(2) 0.34	1.3(4) 0.87		
Sedge	23.9(1) <0.01	2.4(2) 0.30	6.4(2) 0.04	0.4(4) 0.99	8.0(2) 0.02	0.3(2) 0.88	1.2(4) 0.88		
Graminoids	13.9(1) <0.01	2.3(2) 0.31	2.4(2) 0.31	3.8(4) 0.44	3.7(2) 0.16	1.4(2) 0.49	18.9(4) <0.01		
Forbs	1.9(1) 0.17	2.2(2) 0.34	0.4(2) 0.82	9.1(4) 0.06	6.9(2) 0.03	2.4(2) 0.31	1.7(4) 0.79		
Weekly biomass	7.5(1) 0.01	0.7(2) 0.71	3.0(2) 0.22	3.1(4) 0.54	11.3(2) <0.01	5.9(2) 0.05	1.9(4) 0.75		
Sedge	7.5(1) 0.01	1.6(2) 0.45	14.8(2) <0.01	0.1(4) 0.99	9.2(2) 0.01	3.3(2) 0.19	1.7(4) 0.79		
Graminoids	7.0(4) 0.01	2.4(2) 0.30	1.1(2) 0.59	3.9(4) 0.42	5.7(2) 0.06	1.7(2) 0.43	18.3(4) <0.01		
Forbs	0.1(1) 0.75	1.8(2) 0.40	0.7(2) 0.71	7.4(4) 0.12	1.2(2) 0.03	5.6(2) 0.06	2.9(4) 0.57		
<b>2017 – 2018</b>									
Root mass 2-10	-	3.3(2) 0.19	1.3(2) 0.53	2.5(4) 0.65					
Root mass 10-20	-	6.6(2) 0.04	0.6(2) 0.76	4.3(4) 0.36					
Ratio above-/below-ground	-	3.1(2) 0.21	0.7(2) 0.69	2.0(4) 0.74					





## Chapter 4 - Snowmaking in a warmer climate: an in-depth analysis of future water demands for the ski resort *Andermatt-Sedrun-Disentis* (Switzerland) in the 21<sup>st</sup> century

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### Keywords

Climate change scenarios, *Skisim 2.0*, winter tourism, snow reliability, water consumption

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## Abstract

Rising air temperatures threaten the snow reliability of ski resorts. Most resorts rely on technical snowmaking to compensate lacking natural snow. But increased water consumption for snowmaking may cause conflicts with other sectors' water uses such as hydropower production or the hotel industry.

We assessed the future snow reliability (likelihood of a continuous 100-day skiing season and of operable Christmas holidays) of the Swiss resort *Andermatt-Sedrun-Disentis* throughout the 21<sup>st</sup> century, where 65% of the area is currently equipped for snowmaking. Our projections are based on the most recent climate change scenarios for Switzerland (CH2018) and the model *SkiSim 2.0* including a snowmaking module.

Unabated greenhouse gas emissions (scenario RCP8.5) will cause a lack of natural snow at areas below 1800-2000 m asl by the mid-21<sup>st</sup> century. Initially, this can be fully compensated by snowmaking, but by the end of the century the results become more nuanced: While snowmaking can provide a continuous 100-day season throughout the 21<sup>st</sup> century, the economically important Christmas holidays are increasingly at risk under a high-emission scenario in the late 21<sup>st</sup> century. The overall high snow reliability of the resort comes at the cost of an increased water demand. The total water consumption of the resort will rise by 79% by the end of the century (2070-2099 compared to 1981-2010; scenario RCP8.5), implying that new water sources will have to be exploited. Future water management plans at the catchment level, embracing the stakeholders, could help to solve future claims for water in the region.

## Introduction

Winter tourism is an important economic sector in mountain regions. Globally, the European Alps are the number one destination for skiing, with 43% of all skier days worldwide. With 24.9 Mio registered skier days in 2018/19, Switzerland ranks as number six in the world (Vanat 2021). In the winter season 2018/19, the Swiss cable cars yielded revenues of 758 Mio CHF (transport only; SBS 2019), underpinning the substantial economic value.

Rising temperatures due to ongoing and future climate change (Rebetez and Reinhard 2008; IPCC 2018) entail severe reductions in the snow cover (Marty 2008; Klein et al. 2016; NCCS 2018; Hock et al. 2019). For the Swiss Alps, winter and spring temperatures are projected to increase by 1.8 K by the end of the 21<sup>st</sup> century if we drastically reduce greenhouse gas emissions, or even up to 3.9 K without any abatement measures (high-emission scenario). Winter precipitation will progressively fall as rain instead of snow and may increase by 12%. However, the projections for the precipitation increase are less clear than for air temperature (NCCS 2018). Winter runoff will increase and the peak runoff will occur earlier because of earlier snowmelt (Haerberli and Weingartner 2020). The operators of ski areas are thus confronted with major challenges for the future. The snow reliability of resorts has often been assessed by means of the 100-day rule (Witmer 1986, for instance used by Abegg et al. 2007; Scott et al. 2008; Steiger and Abegg 2013), stating that a resort requires at least 100 consecutive days with a sufficient snow cover ( $\geq 30$  cm). However, snow reliability does not necessarily result in economic profitability. Another indicator is the Christmas rule introduced by Scott et al. (2008), specifying that the two weeks over the Christmas and New Year's break are a crucial time period for the operators, as these holidays can yield around one quarter of the revenues (Abegg 1996).

The dominant adaptation strategy of operators to cope with climate change and variability is technical snowmaking (OECD 2007; Gonseth and Vielle 2019; Spandre et al. 2019b; Steiger et al. 2019). Currently, the majority of ski slopes in the European Alps are equipped for snowmaking. According to SBS (2021), the area covered with snowmaking in Switzerland massively increased from 14% (2004) to 48% (2014). Today (2020), 53% of all slopes can be snowed-in technically. This is still markedly less than in Italy (90%) and in Austria (70%), but more than in France (37%). The costs for snowmaking, including the water consumption, are substantial. In Switzerland, these amount to 17% of the daily operating expenses (average for resorts with  $> 25$  Mio CHF revenue; SBS 2021).

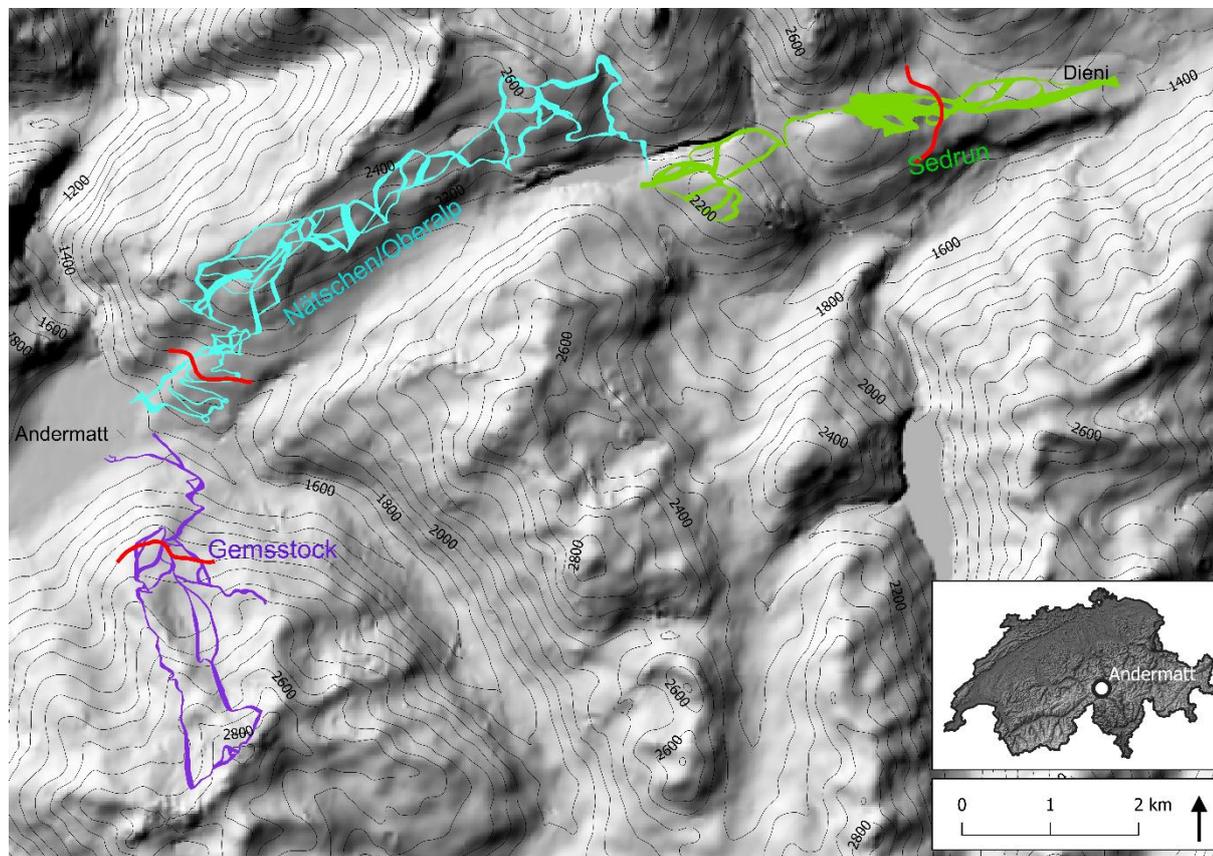
Surveys among stakeholders in the skiing industry have shown that the operators of ski resorts are very aware of climate change (Abegg et al. 2008). Nevertheless, many do not perceive it as an immediate threat and empathise the high priority of economic competition and short-term weather variability as a major cause for revenue fluctuations (Saarinen and Tervo 2006; Hopkins 2015; Abegg et al. 2017). The adaptation strategy to these more short-term challenges is often also technical snowmaking (Trawöger 2014). A study in Austria highlighted a high confidence in snowmaking facilities, even in low-elevation resorts (Wolfsegger et al. 2008). However, increasing temperatures will reduce the snowmaking potential, as high temperatures and/or high relative humidity inhibit the snow production (Willibald et al. 2021). From 1961 to 2020, the number of hours allowing for snowmaking decreased on average by 26% in Austria, with more pronounced reductions at elevations between 1000 and 1500 m asl (Olefs et al. 2020). Nonetheless, water demand is expected to markedly increase by 50% to 110% across the Alps, according to

Steiger et al. (2019). These higher water demands for snowmaking must be put in perspective to water uses in other sectors, such as hydropower production, agriculture, and tourism infrastructures, as well as their future demands under a warmer climate.

The ski resort *Andermatt-Sedrun-Disentis* has recently expanded the ski area with roughly 68 ha of new slopes and with new snowmaking facilities. Such major interventions in the landscape become more and more controversial, especially in times of climate change and a declining demand for ski tickets. Moreover, the short planning horizon of operators does not account for the rising water demand for snowmaking that is very likely under future climatic conditions. Our detailed information about the snowmaking facilities and the snowmaking practices of the operators allow us to present an in-depth analysis of the ski areas future snow reliability throughout the 21<sup>st</sup> century, using the *SkiSim 2.0* model developed by Steiger (2010; based on the *SkiSim 1.0* model by Scott et al. 2003). Based on the RCP (Representative Concentration Pathway) scenarios for Switzerland (CH2018 Project Team 2018), we simulate the future snow cover in the ski area and assess the snow reliability in terms of the 100-day and the Christmas rule. *SkiSim 2.0* includes a snowmaking model, enabling us to estimate the future water consumption for snowmaking. We expect a strong decline in the natural snow reliability by the mid-21<sup>st</sup> century that will likely be compensated by snowmaking. We hypothesise that maintaining the resort's snow reliability will only be feasible at the costs of a strongly enlarged water demand.

## Material and Methods

### The ski resort *Andermatt-Sedrun-Disentis*



**Figure 4. 1** Map with the three ski regions Gemsstock, Nättschen/Oberalp and Sedrun. The red line within each region indicates the critical access elevation, above which skiing is possible even if the lower areas are closed. The miniature map of Switzerland shows the location of Andermatt

The ski resort *Andermatt-Sedrun-Disentis* in the Swiss central Alps has formerly consisted of two separate skiing regions (Gemsstock/Nätschen and Sedrun/Disentis) that were connected by railway from Andermatt to Sedrun/Disentis (Figure 4.1). An ambitious project that was launched in 2005 scheduled the expansion of the ski area along with the construction of luxury hotels, penthouse apartments and a golf course. From 2015 to 2018, 130 to 150 Mio CHF were invested to connect the two ski regions with 68 ha of new ski runs, the construction or replacement of 14 ski lifts and a large-scale expansion of the snowmaking facilities. The entire resort *Andermatt-Sedrun-Disentis* comprises around 270 ha of skiing slopes, 175 ha of which are equipped for snowmaking. With the expansion, the operators obtained an additional concession to build a new reservoir lake and to use ground water in Andermatt whenever the water consumption exceeds the current availability (personal communication with former CEO Silvio Schmid).

The highest point of the ski area is on the Gemsstock at 2961 m asl, the lowest point in Andermatt at 1444 m asl. Because of different snowmaking capacities and different water sources, we divided the ski area with approximately 270 ha of ski runs in three regions: (1) Gemsstock, (2) Nätschen/Oberalp, and (3) Sedrun (Figure 4.1; see Electronic Supplementary Material [Figure S4.1] for the official map).

The region Gemsstock is known for freeriding and has mostly northerly exposed ski runs, partly on the small Gurschen and St. Anna firms. The area that is operative for snowmaking (roughly 27 ha, Table 4.1), is mostly situated below 2100 m asl. The more southerly exposed region of Nätschen/Oberalp (Figure 4.2) includes most of the newly built ski runs and chairlifts. Almost the entire region is now equipped with modern snowmaking facilities featuring the highest water pumping rates (Table 4.1) and with a serviceable area of roughly 99 ha. The highest point of the region is on 2600 m asl. The region Sedrun goes up to 2350 m asl and is the lowest of the three

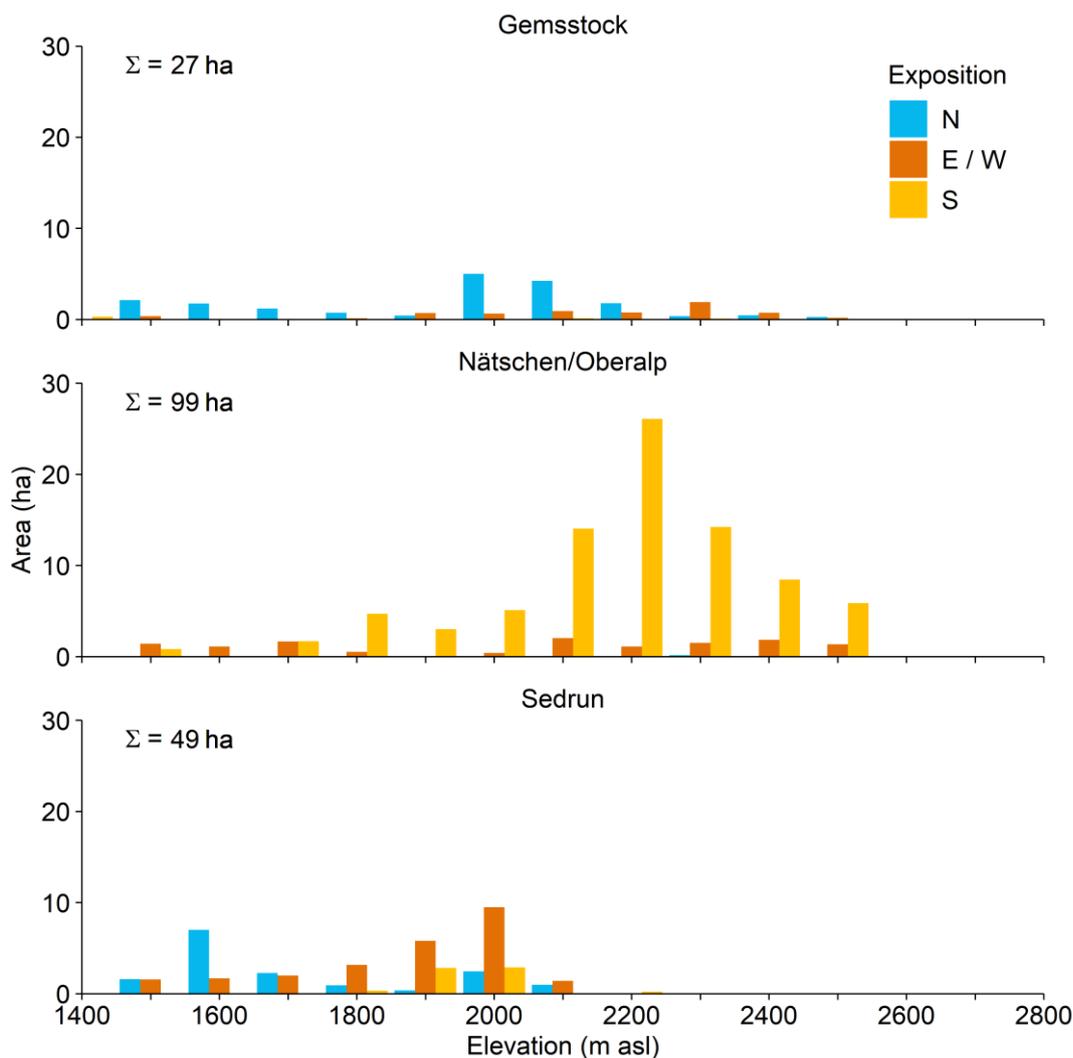
**Table 4.1** Snowmaking information for the three regions of *Andermatt-Sedrun-Disentis*, obtained from the operators

<b>Gemsstock</b>	<b>Season: November - May</b>	
Area with snowmaking (% of total)	27 ha (53%)	
Water extraction	Gurschenbach (river)	Mühle (river)
Usual start of snowmaking	Mid-October	November
Usual end of snowmaking	January	January
Pumping rates	60 L s <sup>-1</sup>	100 L s <sup>-1</sup>
Maximum wet bulb temperature	-1.5 °C	
<b>Nätschen/Oberalp</b>	<b>Season: December - April</b>	
Area with snowmaking (% of total)	99 ha (80%)	
Water extraction	Oberalpsee (lake)	
Usual start of snowmaking	Mid-November	
Usual end of snowmaking	January	
Pumping rates	270 L s <sup>-1</sup>	
Maximum wet bulb temperature	-1.5 °C	
<b>Sedrun</b>	<b>December to April</b>	
Area with snowmaking (% of total)	49 ha (50%)	
Water extraction	Mulinatsch (river)	Val Val (river)
Usual start of snowmaking	November	November
Usual end of snowmaking	January	January
Pumping rates	25 L s <sup>-1</sup>	50 L s <sup>-1</sup>
Maximum wet bulb temperature	-2 °C	

regions. The slopes mainly face towards north or east/west (Figure 4.2), and all facilities for snowmaking in this region have existed already before the investments between 2015 and 2018, covering an area of 49 ha for snowmaking. The infrastructure dates back to the 1990ies. For each of the three regions, we identified a critical access elevation (red line in Figure 4.1) based on the skiing infrastructure. The area above these critical access elevations can be reached via cable cars. Hence, the ski regions may remain operable even if the slopes below these elevations have to stay closed. If the slopes above the critical access elevations become unskiable, the region would not be operational anymore. In the Gemsstock region, the critical access elevation is at 2000 m asl, on Nättschen/Gütsch at 1800 m asl, and in Sedrun at 1900 m asl.

### The model *SkiSim 2.0*

The model *SkiSim 2.0* computes the daily snowpack (in mm water equivalents) considering natural and man-made snow using two modules: (1) a natural snow and (2) a snowmaking module. The natural snow module is a degree day model using daily mean temperature and precipitation as input data. In order to distinguish between snow and rain events and a snow/rain mixture, a lower



**Figure 4.2** The operative areas for snowmaking along the elevational bands and for the aspects north (N), east or west (E / W; together) and south (S) in the three skiing regions. Currently, around 65% of the skiing slopes can be technically snowed-in

and an upper daily mean temperature threshold is calibrated based on daily snow fall data ( $< 1\text{ }^{\circ}\text{C}$ : snow,  $> 3\text{ }^{\circ}\text{C}$ : rain, between: snow/rain mix).

The daily melt is estimated based on degree days (daily mean temperature  $> 0^{\circ}\text{C}$ ). The so-called degree day factor, which describes the melt that occurs per degree day is also fitted during the model calibration process with the number of snow days (snow depth  $\geq 1\text{ cm}$ ) per season (Table S4.1). The number of snow days was slightly overestimated by the model (1.7% in Andermatt and 3.1% in Sedrun; Table 4.2). For further details on the natural snow module refer to Steiger (2010).

The years 1981 to 1987 were used for model calibration and 1988 to 2010 for model evaluation (both periods together denote the reference period). In this application, we used separate degree-day factors for three aspect classes: -25% for north exposed ski slopes, +25% for south exposed slopes and an unchanged calibrated degree-day factor for east and west-facing slopes.

The weather stations Andermatt (1442 m asl; Figure S4.2) and Sedrun (1429 m asl) were used for the input data, Andermatt for the regions Gemsstock and Natschen/Oberalp, and Sedrun for the region Sedrun. Temperature and precipitation are extrapolated from the elevation of these weather stations to the elevation range of the ski areas in 100 m bands. We used a region-specific lapse rate of the air temperature between Sedrun/Gutsch (2287m asl) and Andermatt/Gutsch, respectively, that was fitted during model calibration. Separate lapse rates were calculated for each month of the year, and for dry ( $< 1\text{ mm}$  precipitation) and wet days ( $\geq 1\text{ mm}$ ), respectively. For the precipitation, we assumed a constant 3% increase per 100 m of elevation (Steiger 2010). The snowmaking module takes into account that the operators of the ski area start to produce snow at certain dates (see Table 4.1), provided temperatures are low enough. For comparability with other *SkiSim* studies (e.g., Steiger and Scott 2020) we used  $-2\text{ }^{\circ}\text{C}$  air temperature as threshold for snowmaking. Note that this threshold is rather conservative given the wet-bulb temperature threshold provided by the ski area operators (Table 4.1). For instance, a wet-bulb temperature of  $-2\text{ }^{\circ}\text{C}$  corresponds to  $-1\text{ }^{\circ}\text{C}$  air temperature at 80% humidity, while at 100% humidity no evaporative cooling occurs. Snow is produced until the base layer is 30 cm thick (corresponding to a snow water equivalent of 120 mm at a snow density of  $400\text{ kg m}^{-3}$ ). This is the so-called base-layer snowmaking, which is required for skiing. Thereafter, more snow is produced to sustain skiing until the end of the scheduled season. In the model, the snow production is calculated hourly, under the assumption of interpolated daily minimum and maximum temperatures. Refer to Steiger (2010) for a detailed description of the snowmaking module.

We ran the model for each of the three regions (Gemsstock, Natschen/Oberalp, Sedrun) separately, each divided into elevational bands of 100 m.

We computed the water consumption for a hydrological year that includes the full skiing season (year  $y$  runs from Sept 1<sup>st</sup>  $y-1$  to Aug 31<sup>st</sup>  $y$ ). Based on the daily snowpack, we determined the probability of a continuous snow cover for 100 days in a row (100-day rule) and of a continuous snowpack over Christmas and New Year (Christmas-rule; defined as Dec 22<sup>nd</sup> to Jan 4<sup>th</sup>). As suggested by Abegg et al. (2021), the selection of the snow reliability indicators was done in close co-operation with the ski area operators. Snow reliability and *high* snow reliability are given when the 100-day rule is fulfilled in 70% and 90% of the winters, respectively, as ski areas are expected to be able to withstand single years with less favorable conditions. We defined the snow reliability of the Christmas-rule in the same way. To achieve results that are representative for the entire

regions, we calculated area-weighted means of the probabilities, accounting for the area equipped for snowmaking in the elevational bands and in the aspect classes, as in Steiger and Stötter 2013 (and similar to François et al. 2014, who weighted by ski lift power). The probabilities of each simulation were calculated based on the number of years in the 30-year time period when the 100-day rule or the Christmas rule were fulfilled. If not indicated differently, all reported probabilities refer to the median of all simulations in a RCP scenario (RCP2.6, RCP4.5 and RCP8.5, see below) for a given time period during the 21<sup>st</sup> century (three time periods, see below). When results are visualized for single aspects they always refer to the east/west aspect (north and south aspect in the Supplementary material).

The information about technical issues (area equipped for snowmaking, pumping rates, allowed water extraction) and about snowmaking practices (adopted wet-bulb temperatures, start dates, see Table 4.1) was obtained from *Andermatt-Sedrun-Disentis* directly (formerly *SkiArena Andermatt Sedrun*).

### Climate change scenarios and data availability

The CH2018 climate change scenarios were produced for single weather stations (see Figure S4.2 for the station Andermatt) as well as for a 2 x 2 km grid over whole Switzerland (NCCS 2018). There are three RCP scenarios with a total of 68 simulations: RCP2.6 (greenhouse gas emission stop with warming of less than 2 K compared to pre-industrial times; 12 simulations), RCP4.5 (emission stop in second half of the 21<sup>st</sup> century, warming > 2 K; 25 simulations), and RCP8.5 (high-emission scenario without emission stop; 31 simulations). These scenarios include daily simulations of temperature and precipitation until the year 2099. Here, we present the results for three time periods: 2020-2049 (early century), 2045-2074 (mid-century), and 2070-2099 (end of century). We refer to the 30-year periods of the RCP scenarios to get an estimate of the future conditions under the three scenarios. However, single extreme years may differ significantly from these estimates (for instance, “avalanche winter” 1999, Figure S4.2).

For the weather station in Andermatt, the scenarios for the 21<sup>st</sup> century do not include any simulations for the minimum air temperature. We therefore used the gridded scenarios and extracted the input data for *SkiSim 2.0* (minimum and maximum air temperature, precipitation) from the 2 x 2 km grid cell containing Andermatt. To account for the elevational difference between the grid cell and the weather station, we applied the temperature and precipitation lapse rates of the model.

**Table 4.2** The observed vs. modelled number of days with natural snow cover ( $\geq 1$  cm) for the calibration (1981-1987) and for the validation period (1988-2010) at the stations Andermatt and Sedrun.  $R^2$  is the coefficient of determination for the respective period

	Days with snow cover		
	observed	modelled	$R^2$
<b>Andermatt</b>			
calibration	167.7	166.9	<b>0.89</b>
validation	160.3	163.0	<b>0.83</b>
<b>Sedrun</b>			
calibration	159.1	159.9	<b>0.85</b>
validation	150.3	155.0	<b>0.73</b>

## Water consumption

We modelled the water consumption of the ski area for the reference period of the climate change scenarios (1981 to 2010). Theoretically, these numbers could then be compared to the actual water usage of that period. However, actual water usage is only available for the winters 2002-2017 (Sedrun) and 2014-2017 (Gemsstock). While these numbers refer to the snowmaking facilities of that time, the modelled water consumption is based on the full expansion of the facilities as in 2018. Thus, we could only carry out a plausibility check on the modelled numbers of the water consumption (see result section).

## Results

### Future snow reliability

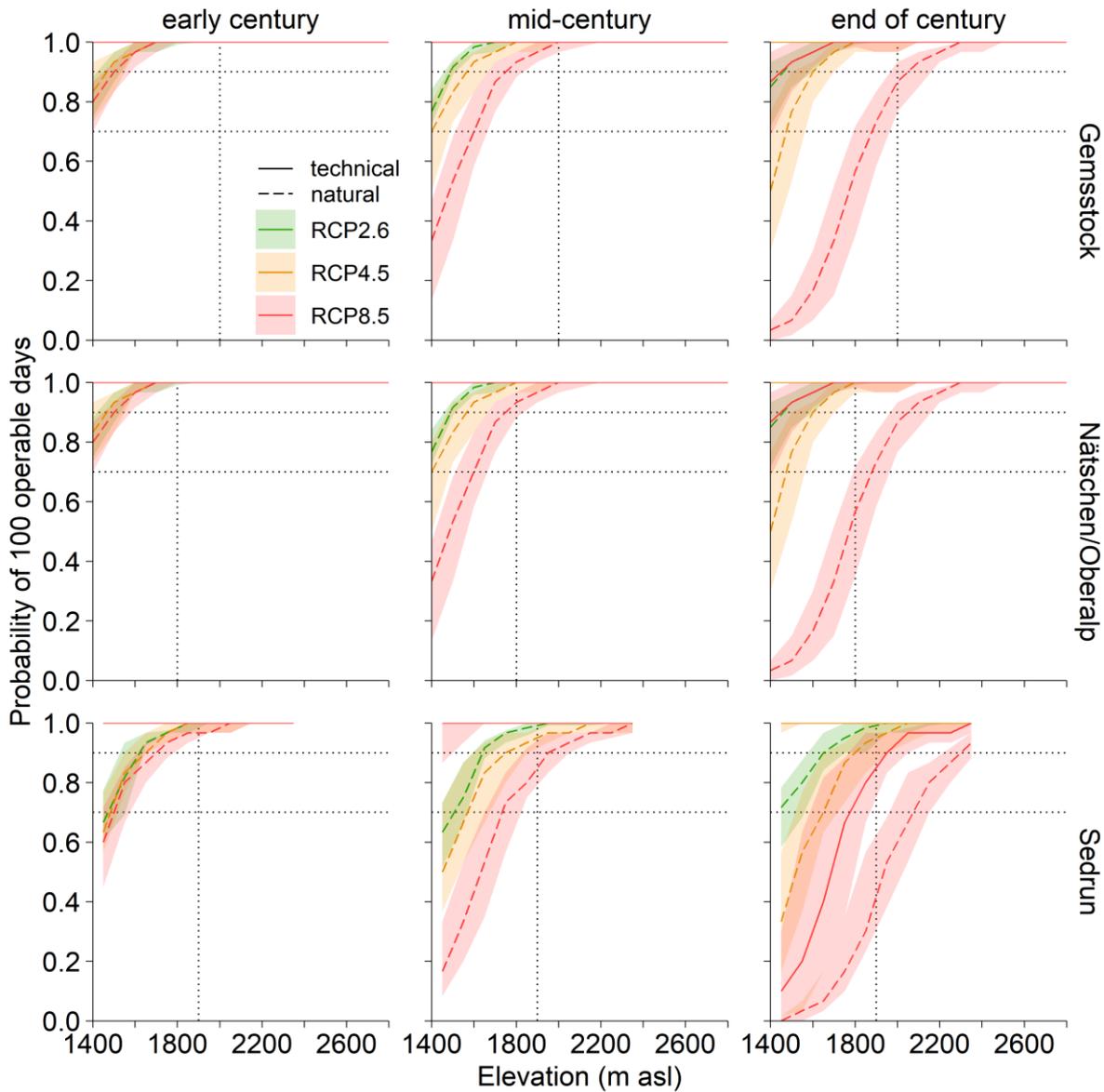
In terms of the 100-day rule and of our 70% threshold, the ski area is naturally snow reliable throughout the early 21<sup>st</sup> century, especially above the critical access elevations (Figure 4.3; see Figure S 4.3 and S4.4 for north and south exposure). Under RCP8.5, the snow reliability below 1700 m asl starts to drop below 70% without any technical snow, but it can be maintained high with snowmaking (Figure S4.5). It continues to decrease towards the end of the 21<sup>st</sup> century, but mainly under RCP8.5. While snowmaking will compensate for the lack of natural snow in the regions of Gemsstock and Nätschen/Oberalp, in Sedrun this will not be feasible at elevations below 1800 m asl (Figure 4.3; east/west exposure). Compared to the east/west aspect, the snow reliability is lower on southerly exposed slopes, especially below the critical access elevation, where the snow reliability is generally lower (natural snow: 13-23%; technical snow: 0-13%; below the critical access elevation under RCP8.5 by end of century) and it is higher on northerly exposed slopes (natural snow: 7-23%, technical snow: 0-10%; Figure S4.4).

The natural snow reliability over the Christmas holidays is generally lower than for an operable season of 100 days (Figure 4.4; see Figure S4.6 and S4.7 for north and south exposure). Snowmaking will mostly allow skiing over the holidays. However, under RCP8.5 Christmas skiing becomes increasingly unlikely by the end of the century (RCP8.5; Figure 4.5). The influence of southerly exposed slopes on the snow reliability is somewhat smaller over the Christmas holidays than for the 100-day rule (natural snow: 3-13%, technical snow: 3-7%; below critical access elevation under RCP8.5, end of century; Figure S4.7). This smaller impact of the exposure is most likely due to lower temperatures in December and January.

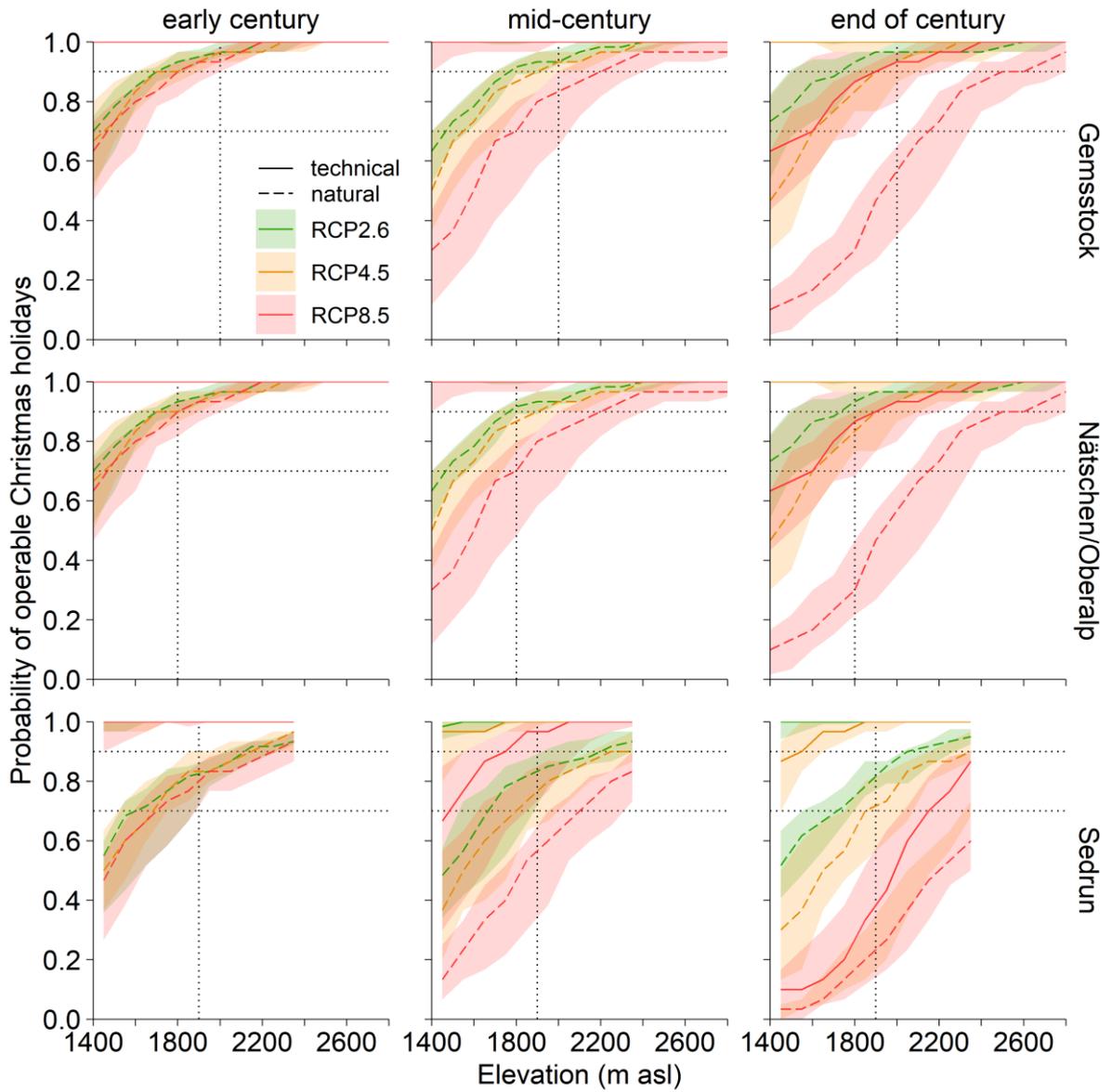
### *Gemsstock*

The natural snow reliability of the Gemsstock region is generally high throughout the whole 21<sup>st</sup> century (100-day rule; Figure 4.3), particularly above the critical access elevation of 2000 m asl. By the end of the century, natural snow will not suffice to sustain a continuous skiing season of 100 days. But this concerns the lower areas under the RCP8.5 scenario only and may be compensated with technical snowmaking (Table 4.3).

The Christmas holidays are snow reliable at the beginning of the century, but the snow reliability gradually decreases towards the end of the 21<sup>st</sup> century (Figure 4.4). Under RCP8.5, the low-elevation areas become snow scarce by the mid-century already (enough natural snow in 56% of the winters only). But with snowmaking, the whole Gemsstock region remains snow reliable until the end of the century (Table 4.3; Figure 4.5 and Figure S4.5).



**Figure 4.3** The probability of **100 consecutive days** that are operable for skiing on natural snow (dashed line) and with technical snow (solid line) for the three regions Gemsstock, Nättschen/Oberalp, Sedrun under the three RCP scenarios and for three time periods of the 21<sup>st</sup> century. The lines represent the median of all simulations per RCP scenario and 50% of the simulations lie in the shaded ribbon. The horizontal lines indicate the snow reliability at 70% and 90%, the vertical lines refer to the critical access elevation. All results refer to an **east/west aspect**, north and south exposures are in Figures S4.3 and S4.4. At a probability of 1, the lines of the three scenarios overlap



**Figure 4.4** The probability that the resort is operable during the **Christmas holidays** on technical snow (solid line) and with natural snow only (dashed line) for the three regions Gemsstock, Nättschen/Oberalp, Sedrun under the three RCP scenarios and for three time periods of the 21<sup>st</sup> century. See legend of Figure 4.3 for a detailed description. All results refer to an **east/west aspect**, north and south exposures are in Figures S4.6 and S4.7

**Table 4.3** The median likelihood (area-weighted) for fulfilling the 100-day and the Christmas rule below and above the critical access elevation, and under three RCP scenarios (R2.6, R4.5, R8.5) for three time periods on natural snow and with snowmaking. Dark green: highly snow reliable, light green: snow reliable, orange: not snow reliable

**Gemsstock – 100-day rule**

Above/below critical access elevation	Snow	early century			mid-century			end of century		
		R2.6	R4.5	R8.5	R2.6	R4.5	R8.5	R2.6	R4.5	R8.5
< 2000 m asl	natural	0.95	0.96	0.94	0.95	0.91	0.77	0.96	0.88	0.36
	technical	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96
≥ 2000 m asl	natural	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	0.97
	technical	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

**Gemsstock – Christmas rule**

< 2000 m asl	natural	0.86	0.84	0.80	0.81	0.79	0.56	0.86	0.73	0.25
	technical	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.78
≥ 2000 m asl	natural	0.99	0.99	0.98	0.98	0.96	0.92	0.97	0.98	0.76
	technical	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98

**Nätschen/Oberalp - 100-day rule**

< 1800 m asl	natural	0.92	0.92	0.89	0.90	0.82	0.59	0.92	0.76	0.11
	technical	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91
≥ 1800 m asl	natural	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	0.83
	technical	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99

**Nätschen/Oberalp - Christmas-rule**

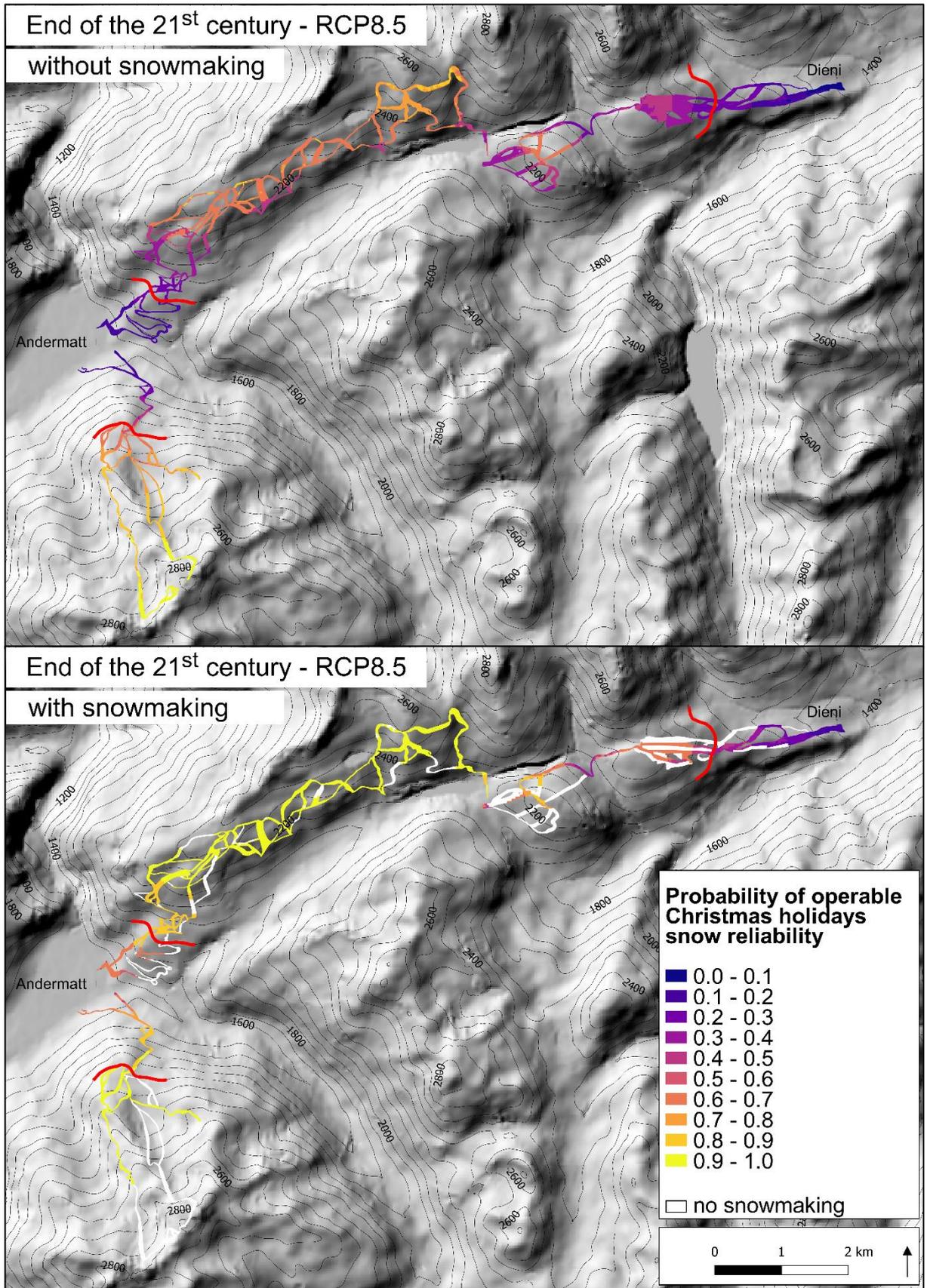
< 1800 m asl	natural	0.80	0.76	0.74	0.74	0.68	0.43	0.89	0.59	0.13
	technical	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	0.68
≥ 1800 m asl	natural	0.96	0.96	0.96	0.94	0.92	0.84	0.96	0.93	0.62
	technical	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	0.93

**Sedrun - 100-day rule**

< 1900 m asl	natural	0.93	0.93	0.89	0.91	0.84	0.66	0.93	0.80	0.20
	technical	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	0.64
≥ 1900 m asl	natural	1.00	1.00	0.99	1.00	0.97	0.91	1.00	0.97	0.60
	technical	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.92

**Sedrun - Christmas-rule**

< 1900 m asl	natural	0.75	0.71	0.72	0.74	0.64	0.40	0.72	0.56	0.12
	technical	1.00	1.00	1.00	1.00	0.99	0.89	1.00	0.96	0.20
≥ 1900 m asl	natural	0.86	0.87	0.84	0.86	0.84	0.64	0.88	0.81	0.35
	technical	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	0.56



**Figure 4.5** The probability of operable Christmas holidays with and without snowmaking at the end of the century under RCP8.5. Areas depicted in white are not serviceable for snowmaking and the red line is the critical access elevation

*Nätschen/Oberalp*

Both, the natural and technical snow reliability of the region Nätschen/Oberalp are similarly high as in the Gemsstock region (100-day rule; Figure 4.3). However, the critical access elevation at 1800 m asl, above where the slopes can be skied unrestrictedly is 200 m lower than on the Gemsstock. Accordingly, under RCP8.5, the low-elevation areas are not naturally snow reliable anymore by the mid-century already. By the end of the century, natural snow is projected to suffice for a 100-day skiing season in one out of ten winters only (Table 4.3). Because of the widespread snowmaking facilities, the region will generally remain snow reliable throughout the whole 21<sup>st</sup> century, even under RCP8.5.

However, the Christmas holidays will likely become increasingly snow scarce (Table 4.3). Below the critical access elevation, producing a base layer of technical snow for Christmas skiing may only be possible in 68% of the winters (RCP8.5).

*Sedrun*

Even though Sedrun is the least snow reliable region (Figure 4.3), the 100-day rule will still be fulfilled throughout most of the 21<sup>st</sup> century. However, from the mid-century on, the natural snow reliability occurs in 66% of the winters below the critical access elevation of 1900 m asl (RCP8.5). With technical snow it can be maintained very high, fulfilling the 100-day rule in 99% of the winters. By the end of the century, the natural snow reliability at low elevations will only be given every fifth winter, and high temperatures will render sufficient snowmaking impossible (only feasible in 64% of the winters; Table 4.3). Above the critical access elevation of 1900 m asl, snowmaking maintains the area snow reliable even under RCP8.5 at the end of the century.

The situation during the Christmas holidays is projected to be considerably worse in Sedrun than in the other two regions Gemsstock and Nätschen/Oberalp (Figure 4.4). By the mid-century, the natural snow reliability at lower elevations will decrease drastically (RCP4.5 and RCP8.5), even above the critical access elevation of 1900 m asl (RCP8.5; Table 4.3). The lack of natural snow can be compensated by snowmaking, but under RCP8.5, the region will not be snow reliable anymore, not even with snowmaking above the critical access elevation (Figure 4.5, Table 4.3).

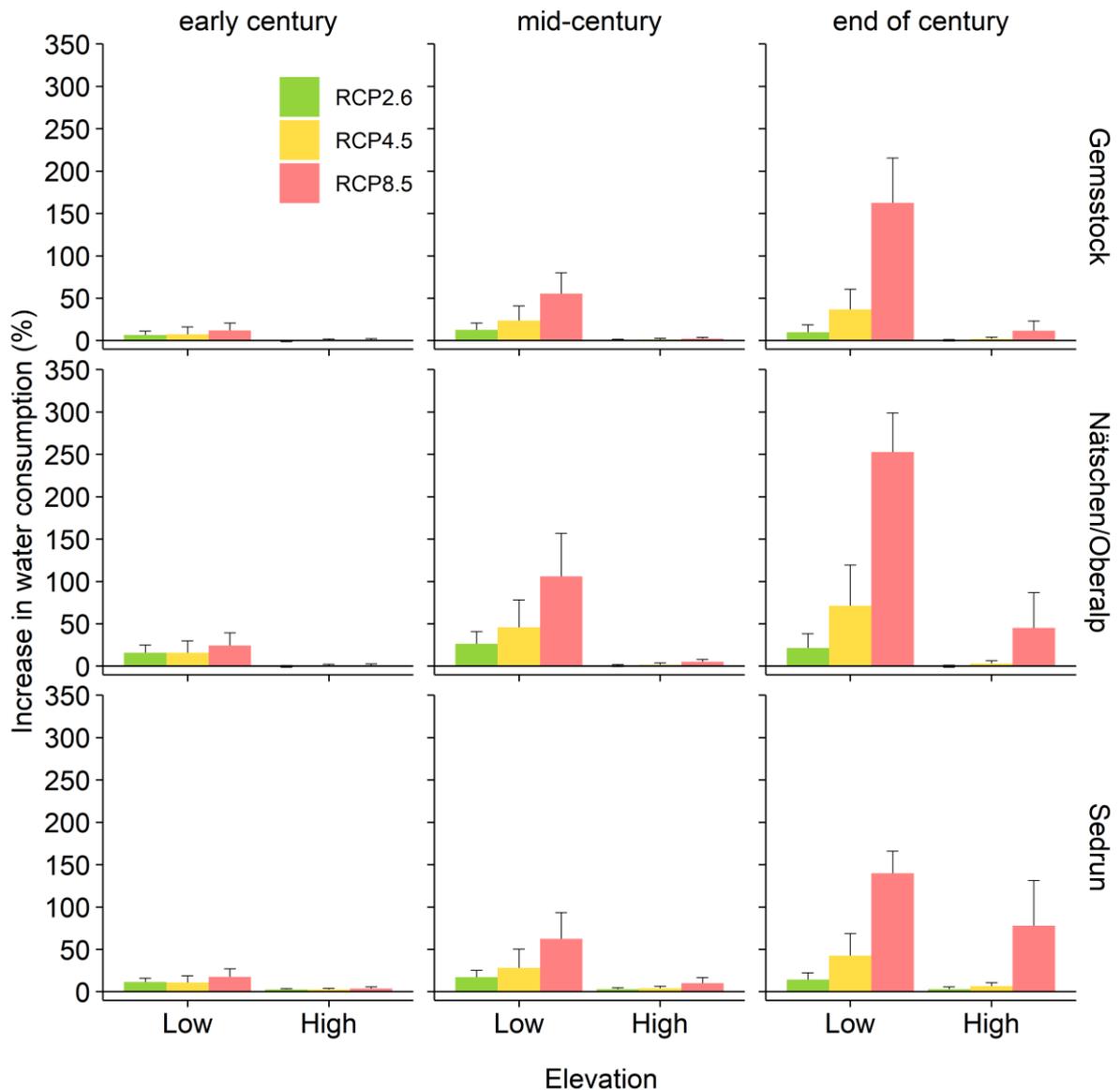
**Water consumption***Water consumption in the reference period*

The mean water consumption in the Gemsstock region between 2014 and 2016 was  $48 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ , whereas in the snow scarce winter of 2017 it was  $150 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ , thus, it more than tripled. In the region Sedrun, the mean water consumption between 2006 and 2016 was  $114 \times 10^3 \text{ m}^3$  and in the winter 2017, it increased by ca. 70% to  $195 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ . For the region Nätschen/Oberalp, the facilities are simply too new to obtain water consumption data of the past winters (running since winter 2019). Because the model assumes a fully expanded ski area, the water consumption of the past years may mainly serve as a plausibility check for the model outcomes.

The modelled baseline water consumption of the three regions of the ski area (reference period 1981-2010) is estimated  $46.8 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  for Gemsstock (17% of the total  $301.5 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ ; 3% lower than observations 2014-2016),  $172.3 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  for Nätschen/Oberalp (57%), and  $82.4 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  for Sedrun (26%), respectively. When we used the temperature and precipitation of the reference period in Sedrun (instead of the RCP climate change

scenarios), the modelled water consumption for the reference period was  $99.0 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  (13% lower than observations 2006-2016).

Our model did not include any “water losses” (see below) and assumed that the operators only produced as much technical snow as required to guarantee a minimum snow depth of 30 cm until the scheduled season ends. However, operators often produce more snow than assumed in our model, as the course of the season is still unknown when the snow is produced (mainly between October/November and January). Thus, our modelled water consumption is rather conservative, and it is therefore likely that our future projections are underestimated.



**Figure 4.6** The increase in water consumption for the three regions compared to the baseline (reference 1981-2010; modelled with full expanded skiing resort). High and low elevations are above and below the critical access elevation, respectively

*Water consumption in the 21<sup>st</sup> century*

The total water consumption at the end of the century will increase by 4% (RCP2.6), 16% (RCP4.5), or even 79% (RCP8.5) compared to the baseline, respectively. Below the critical access elevations (1800-2000 m asl), the relative increase in the water consumption will be much

higher: 15% (RCP2.6), 47% (RCP4.5), and 195% (RCP8.5; reference  $82.1 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ ). Above the critical access elevation, increases in water consumption will only amount to 0% (RCP2.6), 3% (RCP4.5), and 35% (RCP8.5) by the end of the century (reference of  $219.5 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ ).

Hypothetically, the operators could decide to fully abandon snowmaking below the critical access elevations, and only operate the higher areas. This would theoretically diminish the total water consumption of the ski area compared to the reference period, even at the end of the 21<sup>st</sup> century (RCP2.6: -28%, RCP4.5: -25%, RCP8.5: -2%).

If the concentration of greenhouse gas emissions were to stay at today's levels thanks to successfully applied abatement measures (RCP2.6), the total water consumption of the ski area would only be 4% higher than during the reference period by the end of the 21<sup>st</sup> century. Thus, in the following, we report the results of the RCP4.5 and the RCP8.5 scenarios for each region.

### *Gemsstock*

On the Gemsstock, the modelled water consumption for the reference period was  $29.5 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  for areas above the critical access elevation of 2000 m asl, and  $17.3 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  for the lower areas. In line with the high snow reliability throughout the 21<sup>st</sup> century, there is practically no increase in the water consumption above 2000 m asl (+7% by the end of the century under RCP8.5). Below the critical access elevation, including the runs to the valley bottom, the water demand in the mid-century will rise by 22% and 51% under RCP4.5 and RCP8.5, respectively, and by 35% (RCP4.5) and 162% (RCP8.5) by the end of the century (Figure 4.6).

### *Nätschen/Oberalp*

Above the critical access elevation of 1800 m asl, the yearly water consumption was  $146.4 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ , and  $25.9 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  for the lower situated areas during the reference period. In this region, only 9% of the area equipped for snowmaking lies below 1800 m asl (Figure 4.2). As on the Gemsstock, the increase of water consumption above the critical access elevation is moderate (0-5%), except under RCP8.5 at the end of the century with 28%. However, below 1800 m asl, our model projects massive increases in water consumption. Under RCP4.5, these will be 13% (early century), 40% (mid-century) and 61% (end of century), while under RCP8.5 they will even be 24%, 101%, and 271% (Figure 4.6).

### *Sedrun*

In the region Sedrun, the modelled yearly water consumption was  $43.6 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  for elevations above 1900 m asl (critical access elevation), and  $38.9 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  for lower elevations during the reference period. Similar to the other two regions, increases in water consumption will range between 2% to 9%, but under RCP8.5, we project a rise of 78% by the end of the century.

Below 1900 m asl, the water use under RCP4.5 will go up by 39% by the end of the century. Under RCP8.5, the additional water required for snowmaking will increase by 53% in the mid-century, and by 142% by the end of the century (Figure 4.6).

## Discussion

### *Snow reliability*

Our in-depth analysis of *Andermatt-Sedrun-Disentis* show that the ski area remains snow reliable (consecutive 100-day season) in the 21<sup>st</sup> century, provided that snowmaking will be intensified. Fortunately for the operators, the resort as a whole has multiple entry points that are accessible even when lower parts of the ski area might not be skiable anymore. At high elevations, the entire ski area will be fully operational for at least 100 consecutive days. About three quarters of the total ski area lie above 2000 m asl, and this is also where the majority of the new lifts, slopes and ski runs were constructed (2015-2018). Ultimately, only the snow reliability on the valley runs cannot be maintained. The upper parts of the ski areas, including the newly built slopes, are projected to be operable until the end of the 21<sup>st</sup> century.

Due to future climatic conditions and high investment costs for modern snowmaking facilities (Abegg et al. 2008), there will be a diminishing number of operable ski areas in the future worldwide (e.g., Fang et al. 2019; Spandre et al. 2019b; Steiger et al. 2019; Scott et al. 2020). As the snow scarce winters in the late 1980s showed, high-elevation ski areas can benefit from increased visitor numbers when ski areas at lower elevations close (Koenig and Abegg 1997; Steiger et al. 2019). Accordingly, we assume that in the mid-term, *Andermatt-Sedrun-Disentis* may even profit from the shutting down of other ski areas.

In contrast to the minimal season length of 100 consecutive days, the resort's situation over the Christmas holidays (Christmas rule) is much less stable throughout the 21<sup>st</sup> century. Unreliable snow conditions for ski areas during Christmas holidays are projected to emerge globally (Berghammer and Schmude 2014; Steiger et al. 2019; Steiger and Scott 2020), as for instance in 2017, when the onset of snow in Andermatt was on January 3<sup>rd</sup>. In *Andermatt-Sedrun-Disentis*, this mainly affects the region Sedrun, where snowmaking will reach its limits by the end of the century. In a comprehensive analysis of 34 ski areas in the canton of Grisons (eastern Switzerland), Abegg et al. (2015) used the same 70% threshold for the 100-day and the Christmas rule for assessing the snow reliability and highlighted that only 15% of the ski areas would be naturally snow reliable by the end of the century. Snowmaking could increase the share of snow reliable ski areas to 56%, but the required snow production would rise by more than 100%. Sedrun was one of the analysed ski areas and they projected that with snowmaking, the ski area would still be snow reliable by the end of the 21<sup>st</sup> century. Our results with a higher spatial resolution and with the latest version of the Swiss climate change scenarios revealed that the ski area will only be partially snow reliable, fulfilling the 100-day rule, but not the Christmas rule anymore. The low snow reliability in the region Sedrun is partly due to older snowmaking facilities compared to Gemsstock and Nätschen/Oberalp. The technical snow reliability could be increased by renewing these old facilities and thereby allowing for higher water pumping rates (pumping rates at Nätschen/Oberalp are between five to ten times higher than those in Sedrun). This is underpinned by the very snow scarce winter of 2017. While the water consumption in the Gemsstock region tripled, in the region of Sedrun there was an increase of roughly 70% only. It is likely that the older snowmaking facilities restricted the production of technical snow. This reinforces a study across six Norwegian ski resorts, where lower snowmaking capacities were related to a higher vulnerability over the Christmas holidays (Dannevig et al. 2021). However, the natural snow reliability was also lower in Sedrun, therefore, the lower overall snow reliability cannot be attributed to the older snowmaking facilities alone. Generally, there has been a rapid technical

development of such facilities, as evidenced by the high pumping rates of the new installations in Nätschen/Oberalp ( $270 \text{ L s}^{-1}$ ). Such a high performance, in combination with sufficient water supply, is considered crucial for the snow reliability in snow scarce years. Even though further gains in the efficiency of snowmaking facilities are likely, the technology itself is also bound to physical limitations (wet-bulb temperature). Hence, unsuitable climatic conditions as they are often observed at the beginning of the season and/or at low elevations, substantially reduce the potential benefit of snowmaking facilities (Berard-Chenu et al. 2022).

#### *Water consumption*

Generally, the water consumption for snowmaking in the European Alps is estimated to increase between 50 and 110% (by 2050; Steiger et al. 2019). A rising demand for technical snow causes higher costs for the water consumption, but also increased operating costs and additional investments in snowmaking facilities. We project that in an average winter at the end of the century, the entire resort *Andermatt-Sedrun-Disentis* will require 79% more water for snowmaking (RCP8.5; roughly an increase from  $300 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  to  $540 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ ). When we take the  $730 \text{ L day}^{-1}$  water consumption of a typical 4-person household as a reference (Abwasser Uri 2019), the water consumption for snowmaking would increase from approximately 1130 to 2020 households. Further investment in the snowmaking capacity would intensify the water consumption beyond our model results. In the French Alps, the water consumption by the end of the century could even increase by the ninefold, if the area for snowmaking would be increased to 100% (Spandre et al. 2019a).

The model *SkiSim 2.0* does not account for water losses through wind drift, sublimation and evaporation, which may lead to the underestimation of the water consumption during the process of snowmaking. Grünewald and Wolfsperger (2019) highlighted that water losses ranged between 7 and 35%, depending on weather conditions. In their field tests, water losses augmented by 2.8% per 1 K increase in air temperature. Future conditions for snowmaking will become increasingly unfavourable and hence, future water losses are very likely to increase. Nevertheless, our model results indicate a rather moderate increase in water consumption compared to other ski areas in Switzerland and Austria. For Scuol (eastern Alps, CH), the water consumption by the end of the century may rise by a factor of 2.4-5, in Hochjoch (AU) by a factor of 2.2-3.7 (Abegg and Steiger 2016). For the winter season 2007 in the winter tourism region Davos (CH), Rixen et al. (2011) compared the water and energy consumption of the ski resort with the drinking water and energy consumption of the municipality. In terms of energy consumption, the ski resort used less than 1% of the municipality's energy. But the water use comprised 21.5% of the municipalities drinking water (but using different water sources).

The percental upsurge in water consumption for the region Nätschen/Oberalp, where most of the new ski runs, lifts, and snowmaking facilities were built, is similar as the percental increase for the whole ski area (+19% by the mid-century and +65% by the end of the century, RCP8.5). Most of the water for snowmaking is extracted from the reservoir lake Oberalpsee (max.  $200 \times 10^3 \text{ m}^3 \text{ season}^{-1}$  extraction, pumping rate of  $270 \text{ L s}^{-1}$ ). Potential future water resources would be an additional reservoir lake ("Ober Gütsch",  $50 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ ) and groundwater in Andermatt ( $200 \times 10^3 \text{ m}^3 \text{ season}^{-1}$ ). With unabated greenhouse gas emissions (RCP8.5 scenario), the reservoir Oberalpsee will suffice for the snowmaking activities of the region until the mid-century, but the

water demand will clearly exceed the availability by the end of the century. Additional water resources in the range of  $80 \times 10^3 \text{ m}^3$  without any water losses will be required. Noteworthy, if we reduce the greenhouse gas emissions (RCP4.5), the reservoir of the Oberalpsee will still meet the water demands for snowmaking even by the end of the century. As the other regions' water sources are rivers, the water availability is much more constrained by interannual fluctuations and there are no defined maximum rates of extraction per year (residual water flows in rivers have to be guaranteed).

### *Competition for water*

The Oberalpsee is also used for hydroelectric power generation. The power station Oberalp produces three quarters of the energy during snowmelt and the subsequent summer months without snow. The withdrawal of water by the ski resort and by the electrical power company is regulated by law (Elektrizitätswerk Ursern 2020). Hence, competition and conflicts between the hydro-power production and snowmaking will arise if the water level of the Oberalpsee and rivers will drop in the future. Such conflicts may emerge mainly in drier regions of Switzerland, such as the Engadine or parts of the Valais. Peaks in water demand for tourism often coincide with generally low water levels (Reynard 2020). Nevertheless, water shortages in Swiss tourism regions are usually caused by unsustainable water management strategies and poor distribution among stakeholders, not by a general lack of water (Clivaz and Reynard 2008; Schneider et al. 2016). A detailed study for the French Isère department showed that the water availability for snowmaking may even increase due to more rain and increased snowmelt, but mainly at catchment areas below 1500 m asl (Gerbaux et al. 2020). In the region of Andermatt, the newly built resort including golf, swimming pools and spa have generated new water demands that have not yet been quantified. We therefore suggest that the increasing water consumption of the ski resort as well as these new sources of water demand are considered in future water management strategies.

In addition to the new demands for water and the climatic changes, there are changes in the land use of the Ursern valley that affect the surface runoff of the catchment. Successive abandoning of extensive grazing on alpine grassland is leading to an expansion of shrubland, in particular of the green alder. Because of the higher evapotranspiration of the green alder and abandoned grassland, this land use change reduces the runoff in the Ursern catchment (Inauen et al. 2013; van den Bergh et al. 2018). However, land use changes primarily affect the runoff during the summer months. Snowmaking usually starts in mid-November or early December and commonly lasts until January. Alaoui et al. (2014) showed that the water discharge of the Ursern valley during these months is clearly dominated by precipitation. As the amount of winter precipitation is expected to shift by -2 to 24% by the end of the century (NCCS 2018), future competition for water resources in winter will likely not be triggered by a decrease in the supply, but rather by increasing water demands of the ski areas.

## Conclusions

The studied ski resort *Andermatt-Sedrun-Disentis* features a high natural snow reliability throughout the 21<sup>st</sup> century and reductions in natural snow can mainly be compensated by snowmaking. However, under a climate change scenario with unabated emissions, lower areas (below 1800-1900 m asl) as well as the region of Sedrun, even above the critical access elevation, will not be snow-reliable over the Christmas holidays by the end of the 21<sup>st</sup> century, as the climate will not

allow for sufficient snow production. Under this scenario, the water consumption will rise by 79% by the end of the century. The currently largest water source, the reservoir lake Oberalpsee, will then not meet the water demands of the region anymore and new sources such as ground water and a new reservoir lake will have to be exploited. According to the climate change scenarios (CH2018) it is likely that the water supply during the months of highest water consumption (November until January) will not decrease, but the high consumption may lead to competition with other sectors such as hydropower or the new hotels. Although the overall demand for skiing tourism in Switzerland has been decreasing since 2008 (SBS 2021), the comparative advantage of *Andermatt-Sedrun-Disentis* (Steiger and Abegg 2018) – in combination with the significant expansion of the resort – will likely lead to an increase in tourist numbers.

## References

- Abegg B (1996) Klimaänderung und Tourismus: Klimafolgenforschung am Beispiel des Wintertourismus in den Schweizer Alpen. Vdf Hochschulverlag, Zurich. p 222
- Abegg B, Agrawala S, Crick F, de Montfalcon A (2007) Climate change impacts and adaptation in winter tourism. In: Agrawala S (ed) *Climate change in the European Alps - Adapting winter tourism and natural hazards management*. OECD, pp 25–60
- Abegg B, Kolb M, Sprengel D, Hoffmann VH (2008) Klimawandel aus der Sicht der Schweizer Seilbahnunternehmer. In: Bieger T (ed) *Jahrbuch der Schweizerischen Tourismuswirtschaft*. St. Gallen, pp 73–83
- Abegg B, Morin S, Demiroglu OC, François H, Rothleitner M, Strasser U (2021) Overloaded! Critical revision and a new conceptual approach for snow indicators in ski tourism. *Int J Biometeorol* 65:691–701. doi: 10.1007/s00484-020-01867-3
- Abegg B, Steiger R (2016) Klimawandel und Wintertourismus: Zwei benachbarte Skigebiete im Vergleich. In: Aistleitner J (ed) *Innsbrucker Geographische Studien, Band 40: Die Welt verstehen – eine geographische Herausforderung. Eine Festschrift der Geographie Innsbruck für Axel Borsdorf*. Innsbrucker Studienkreis für Geographie, Innsbruck, pp 391–400
- Abegg B, Steiger R, Trawöger L (2017) Resilience and perceptions of problems in alpine regions. In: Butler RW (ed) *Tourism and Resilience*. CABI Publications, Wallingford, pp 105–117
- Abegg B, Steiger R, Walser R (2015) Aktuelle und zukünftige Schneesicherheit der Skigebiete in Graubünden [Current and future snow reliability of the ski resorts in Grison]. In: T. Bieger, P. Beritelli CL (ed) *St. Galler Schriften für Tourismus und Verkehr: Vol. 6. Schweizer Jahrbuch für Tourismus 2014–15*. ESV, Berlin, pp 47–61
- Abwasser Uri (2019) *Geschäftsbericht 2019*. p 27
- Alaoui A, Willmann E, Jasper K, Felder G, Herger F, Magnusson J, Weingartner R (2014) Modelling the effects of land use and climate changes on hydrology in the Ursern Valley, Switzerland. *Hydrol Process* 28:3602–3614. doi: 10.1002/hyp.9895
- Berard-Chenu L, François H, George E, Morin S (2022) Past changes in natural and managed snow reliability of French Alps ski resorts from 1961 to 2018. *Cryosph* 863–881. doi: <https://doi.org/10.5194/tc-16-863-2022>
- Berghammer A, Schmude J (2014) The christmas-easter shift: Simulating alpine ski resorts' future development under climate change conditions using the parameter "optimal ski day." *Tour Econ* 20:323–336. doi: 10.5367/te.2013.0272
- CH2018 Project Team (2018) CH2018 - Climate Scenarios for Switzerland. Natl. Cent. Clim. Serv.

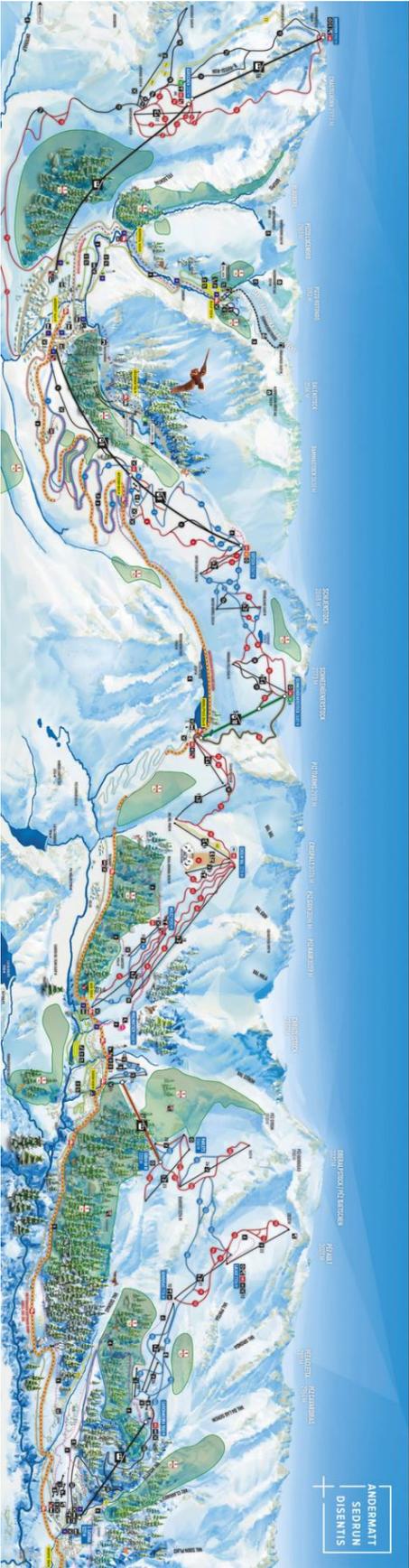
- Clivaz C, Reynard E (2008) Crans-Montana: Water resources management in an alpine tourist resort. In: Wiegandt E (ed) *Mountains: Sources of water, sources of knowledge*. Advances in Global Change Research, vol 31. Springer, Dordrecht, pp 103–119
- Dannevig H, Gildestad IM, Steiger R, Scott D (2021) Adaptive capacity of ski resorts in Western Norway to projected changes in snow conditions. *Curr Issues Tour* 24:3206–3221. doi: 10.1080/13683500.2020.1865286
- Elektrizitätswerk Ursern (2020) Gotthard Energie - Strom aus Wasserkraft. In: EWU. <https://www.ew-ursern.ch/energie/wasserkraft/>. Accessed 13 Aug 2020
- Fang Y, Scott D, Steiger R (2019) The impact of climate change on ski resorts in China. *Int J Biometeorol* 65:677–689. doi: 10.1007/s00484-019-01822-x
- François H, Morin S, Lafaysse M, George-Marcelpoil E (2014) Crossing numerical simulations of snow conditions with a spatially-resolved socio-economic database of ski resorts: A proof of concept in the French Alps. *Cold Reg Sci Technol* 108:98–112. doi: 10.1016/j.coldregions.2014.08.005
- Gerbaux M, Spandre P, François H, George E, Morin S (2020) Snow reliability and water availability for snowmaking in the ski resorts of the Isère Département (French Alps), under current and future climate conditions. *J Alp Res* 108:1–19. doi: 10.4000/rga.6742
- Gonseth C, Vielle M (2019) A general equilibrium assessment of climate change impacts on Swiss winter tourism with adaptation. *Environ Model Assess* 24:265–277. doi: 10.1007/s10666-018-9641-3
- Grünewald T, Wolfsperger F (2019) Water losses during technical snow production: Results from field experiments. *Front Earth Sci* 7:1–13. doi: 10.3389/feart.2019.00078
- Haeberli W, Weingartner R (2020) In full transition: Key impacts of vanishing mountain ice on water-security at local to global scales. *Water Secur* 11:100074. doi: 10.1016/j.wasec.2020.100074
- Hock R, Rasul G, Adler C, Cáceres B, Gruber S, Hirabayashi Y, Jachson M, Käab A, Kang S, Kutuzov S, Milner A, Molau U, Morin S, Orlove B, Steltzer H (2019) High mountain areas. In: H. O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama NMW (ed) *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. World Meteorological Organization, in press, p 202
- Hopkins D (2015) The perceived risks of local climate change in Queenstown, New Zealand. *Curr Issues Tour* 18:947–965. doi: 10.1080/13683500.2013.776022
- Inauen N, Körner C, Hiltbrunner E (2013) Hydrological consequences of declining land use and elevated CO<sub>2</sub> in alpine grassland. *J Ecol* 101:86–96. doi: 10.1111/1365-2745.12029
- IPCC (2018) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner H, et al. (eds) *Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change*. Geneva, Switzerland, pp 374–381
- Klein G, Vitasse Y, Rixen C, Marty C, Rebetez M (2016) Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than later snow onset. *Clim Change* 139:637–649. doi: 10.1007/s10584-016-1806-y
- Koenig U, Abegg B (1997) Impacts of climate change on winter tourism in the Swiss Alps. *J Sustain Tour* 5:46–58. doi: 10.1080/09669589708667275

- Marty C (2008) Regime shift of snow days in Switzerland. *Geophys Res Lett* 35:L12501. doi: 10.1029/2008GL033998
- NCCS (2018) *Klimaszenarien für die Schweiz CH2018*. National Centre for Climate Services. Zurich
- OECD (2007) *Climate change in the European Alps. Adapting winter tourism and natural hazards management*. Paris. p 136
- Olefs M, Koch R, Schöner W, Marke T (2020) Changes in snow depth, snow cover duration, and potential snowmaking conditions in Austria, 1961-2020 - a model based approach. *Atmosphere* 11:1330. doi: 10.3390/atmos11121330
- Rebetez M, Reinhard M (2008) Monthly air temperature trends in Switzerland 1901-2000 and 1975-2004. *Theor Appl Climatol* 91:27–34. doi: 10.1007/s00704-007-0296-2
- Reynard E (2020) Mountain tourism and water and snow management in climate change context. *J Alp Researach* 801:1–7. doi: 10.4000/rga.6816
- Rixen C, Teich M, Lardelli C, Gallati D, Pohl M, Pütz M, Bebi P (2011) Winter tourism and climate change in the Alps: An assessment of resource consumption, snow reliability, and future snowmaking potential. *Mt Res Dev* 31:229–236. doi: 10.1659/MRD-JOURNAL-D-10-00112.1
- Saarinen J, Tervo K (2006) Perceptions and adaptation strategies of the tourism industry to climate change: The case of Finnish nature-based tourism entrepreneurs. *Int J Innov Sustain Dev* 1:214–228. doi: 10.1504/IJISD.2006.012423
- SBS (2019) *Saisonbilanz 2018/19. Frequentierung der Skigebiete*. Bern. p 24
- SBS (2021) *Fakten & Zahlen zur Schweizer Seilbahnbranche 2021*. Bern. p 35
- SBS (2020) *Fakten & Zahlen zur Schweizer Seilbahnbranche 2020*. Bern. p 38
- Schneider F, Bonriposi M, Graefe O, Herweg K, Homewood C, Huss M, Kauzlaric M, Liniger H, Rey E, Reynard E, Rist S, Schädler B, Weingartner R (2016) *MontanAqua: Tackling water stress in the Alps. Water management options in the Crans-Montana-Sierre regions (Valais)*. *GAIA* 25/3:191–193
- Scott D, Dawson J, Jones B (2008) Climate change vulnerability of the US Northeast winter recreation-tourism sector. *Mitig Adapt Strateg Glob Chang* 13:577–596
- Scott D, McBoyle G, Mills B (2003) Climate change and the skiing industry in southern Ontario (Canada): Exploring the importance of snowmaking as a technical adaptation. *Clim Res* 23:171–181. doi: 10.3354/cr023171
- Scott D, Steiger R, Dannevig H, Aall C (2020) Climate change and the future of the Norwegian alpine ski industry. *Curr Issues Tour* 23:2396–2409. doi: 10.1080/13683500.2019.1608919
- Spandre P, François H, Verfaillie D, Lafaysse M, Déqué M, Eckert N, George E, Morin S (2019a) Climate controls on snow reliability in French Alps ski resorts. *Sci Rep* 9:1–9. doi: 10.1038/s41598-019-44068-8
- Spandre P, François H, Verfaillie D, Pons M, Vernay M, Lafaysse M, George E, Morin S (2019b) Winter tourism under climate change in the pyrenees and the French alps: Relevance of snowmaking as a technical adaptation. *Cryosph* 13:1325–1347. doi: 10.5194/tc-13-1325-2019
- Steiger R (2010) The impact of climate change on ski season length and snowmaking requirements in Tyrol, Austria. *Clim Res* 43:251–262. doi: 10.3354/cr00941
- Steiger R, Abegg B (2013) The sensitivity of Austrian ski areas to climate change. *Tour Plan Dev* 10:480–493. doi: 10.1080/21568316.2013.804431

- Steiger R, Abegg B (2018) Ski areas' competitiveness in the light of climate change: comparative analysis in the Eastern Alps Robert. In: Müller D, Więckowski M (eds) *Tourism in transition, recovering from decline and managing change*. Springer International Publishing, Basel, pp 187–199
- Steiger R, Scott D (2020) Ski tourism in a warmer world: Increased adaptation and regional economic impacts in Austria. *Tour Manag* 77:104032. doi: 10.1016/j.tourman.2019.104032
- Steiger R, Scott D, Abegg B, Pons M, Aall C (2019) A critical review of climate change risk for ski tourism. *Curr Issues Tour* 22:1343–1379. doi: 10.1080/13683500.2017.1410110
- Steiger R, Stötter J (2013) Climate change impact assessment of ski tourism in Tyrol. *Tour Geogr* 15:577–600. doi: 10.1080/14616688.2012.762539
- Trawöger L (2014) Convinced, ambivalent or annoyed: Tyrolean ski tourism stakeholders and their perceptions of climate change. *Tour Manag* 40:338–351. doi: 10.1016/j.tourman.2013.07.010
- van den Bergh T, Körner C, Hiltbrunner E (2018) Alnus shrub expansion increases evapotranspiration in the Swiss Alps. *Reg Environ Chang* 18:1375–1385. doi: 10.1007/s10113-017-1246-x
- Vanat L (2021) 2021 International Report on Snow & Mountain Tourism. Overview of the key industry figures for ski resorts. p 245
- Willibald F, Kotlarski S, Ebner PP, Bavay M, Marty C, Trentini F V., Ludwig R, Grêt-Regamey A (2021) Vulnerability of ski tourism towards internal climate variability and climate change in the Swiss Alps. *Sci Total Environ* 784:147054. doi: 10.1016/j.scitotenv.2021.147054
- Witmer U (1986) Erfassung, Bearbeitung und Kartierung von Schneedaten in der Schweiz. Geographisches Institut der Universität Bern, Bern. p 215
- Wolfsegger C, Gössling S, Scott D (2008) Climate Change Risk Appraisal in the Austrian Ski Industry. *Tour Rev Int* 12:13–23. doi: 10.3727/154427208785899948

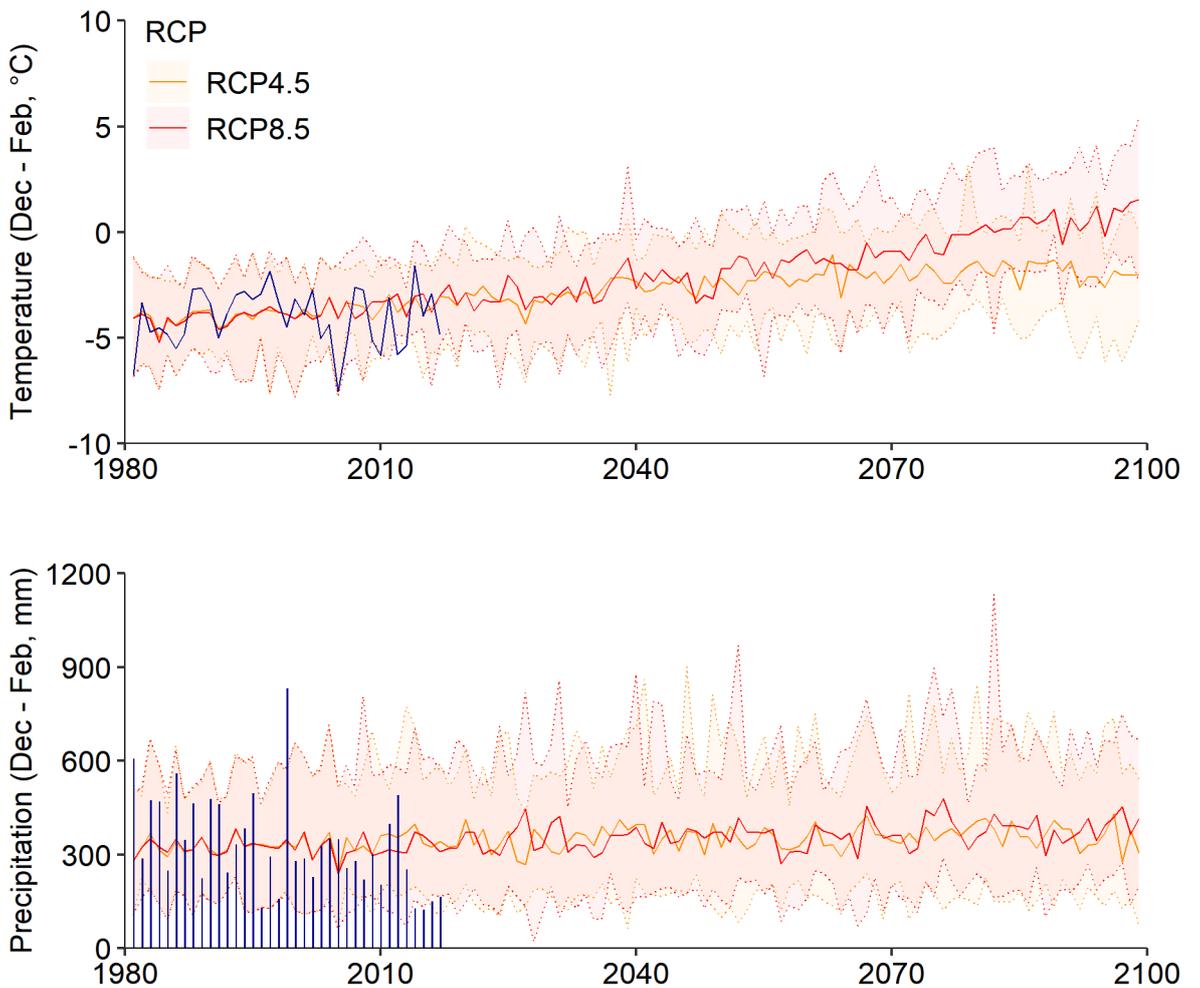
Supplemental material for chapter 4

Figure S4.1 Map of the ski resort (<https://andermatt-sedrun-disentis.ch/>; accessed July 22<sup>nd</sup>, 2020)

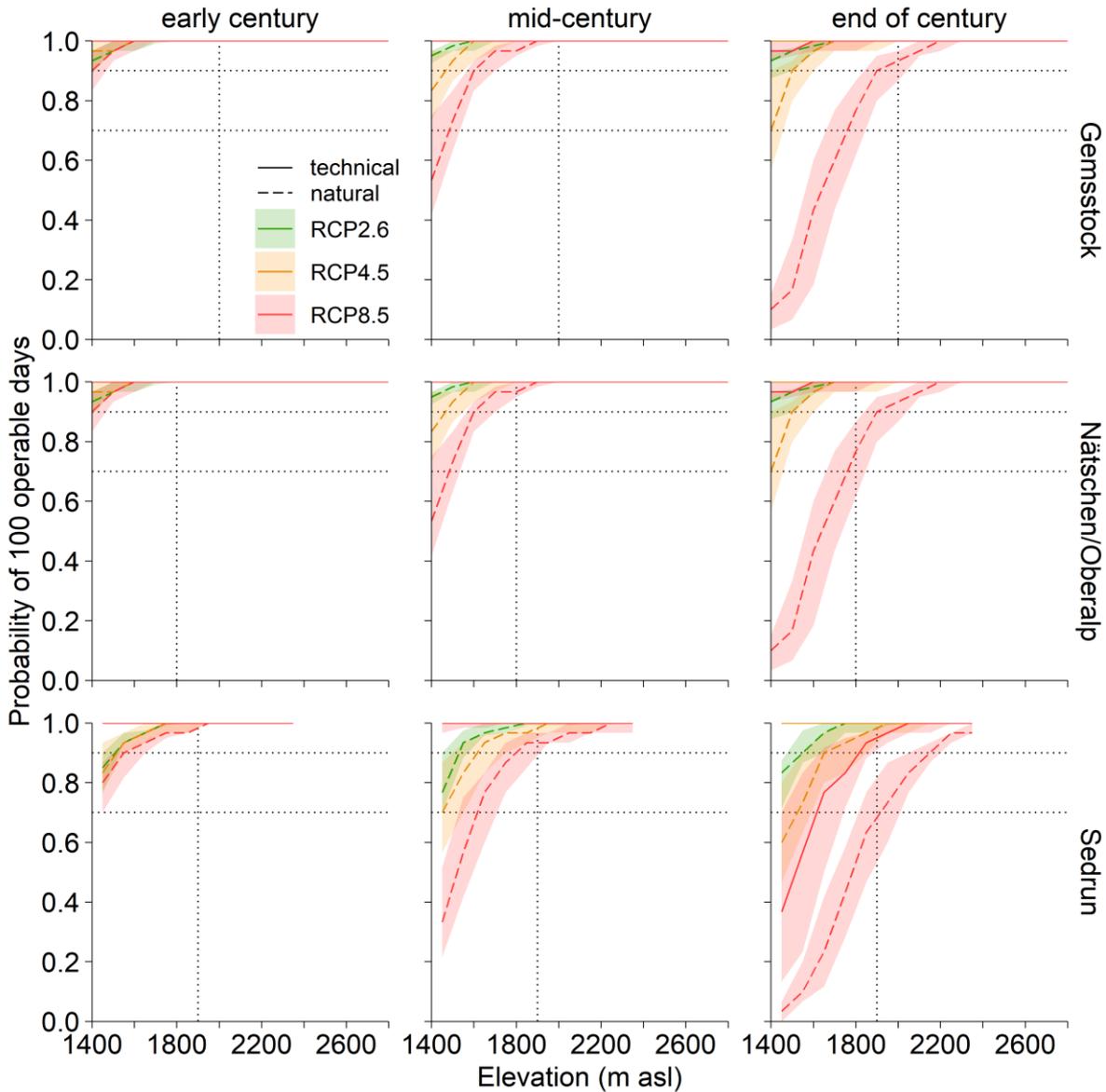


**Table S4.1** The calibrated degree-day factors (in mm water equivalents / K) for the aspect classes and the two weather stations Andermatt and Sedrun

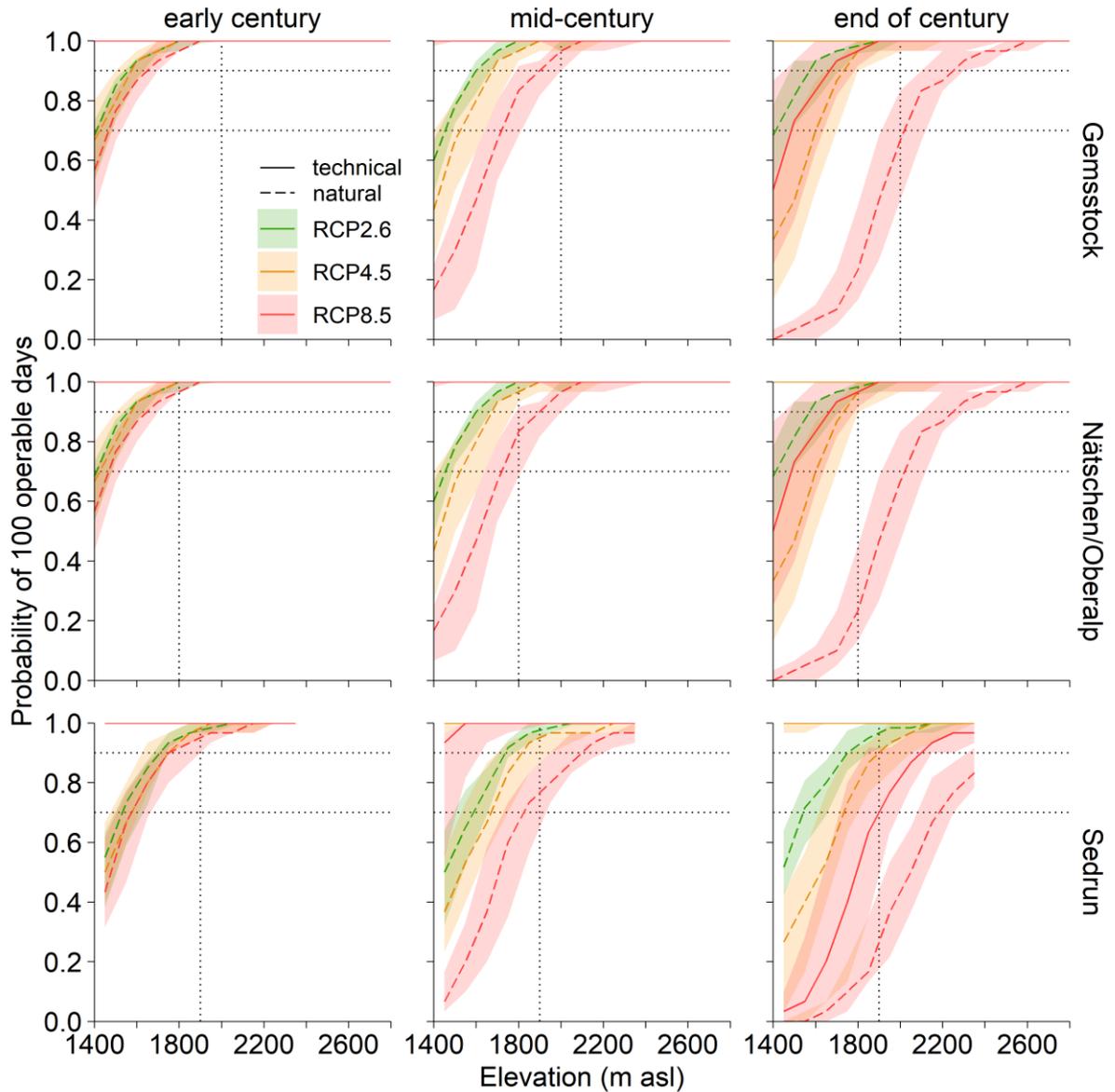
	North		East / west aspect		South	
	min	max	min	max	min	max
Andermatt	0.7	3.3	1.0	5.0	1.5	7.5
Sedrun	0.8	3.4	1.2	5.2	1.8	7.8



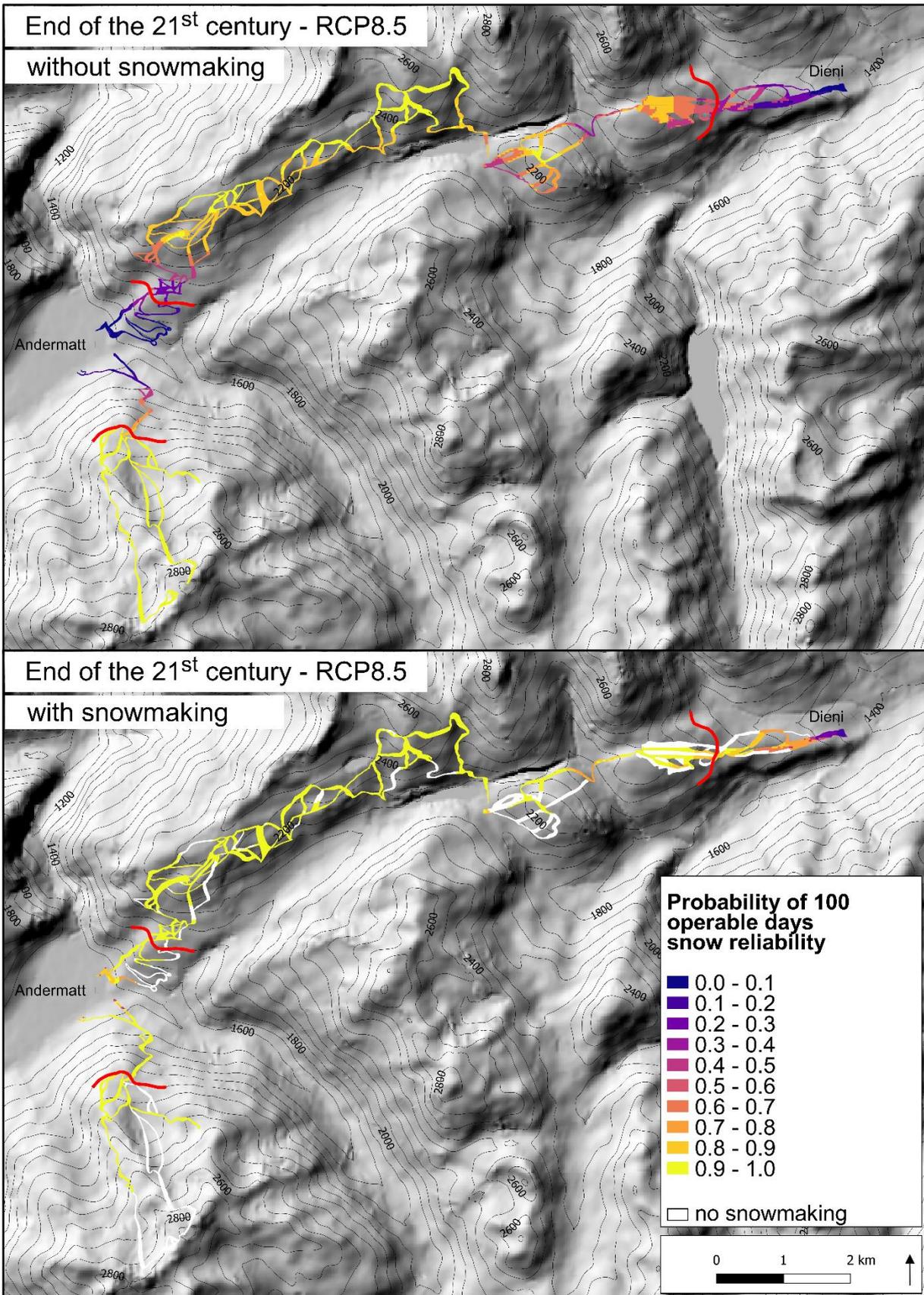
**Figure S4.2** Mean winter temperature and the winter precipitation sum (December to February) at the weather station Andermatt (1442 m asl). Measured temperature and precipitation are shown in dark blue (Federal Office of Meteorology and Climatology MeteoSwiss, (1981-2017, period refers to the start of the reference period of the climate change scenarios until last season's data of water usage for snowmaking). The mean, minimum and maximum of all simulations of the Swiss climate change scenarios (NCCS, 2018) are depicted in orange (RCP4.5) and red (RCP8.5, 1981-2099)



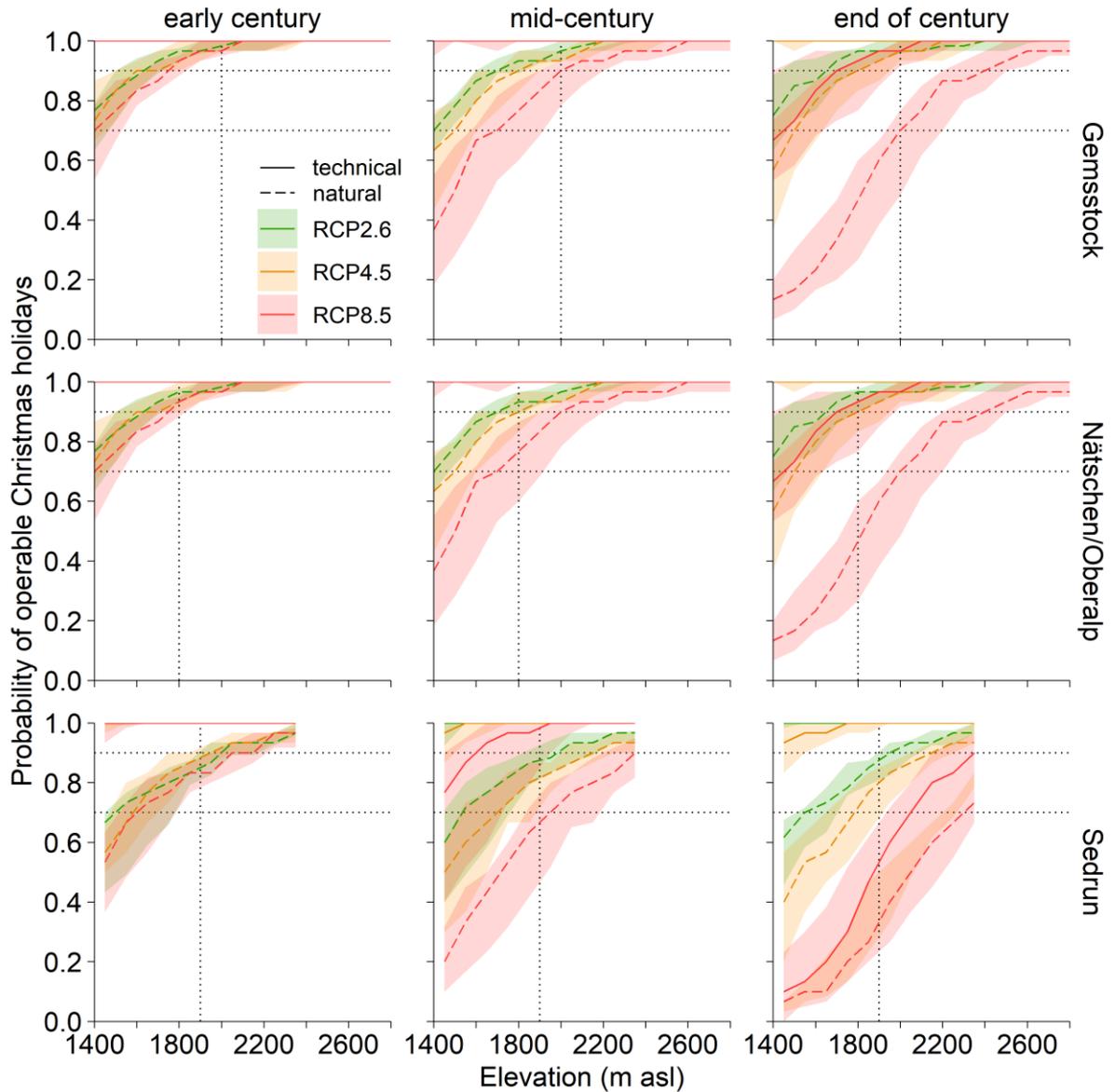
**Figure S4.3** The probability of **100 consecutive days** that are operable for skiing on natural snow (dashed line) and with technical snow (solid line) for the **north**-exposed slopes of the three regions Gemsstock, Nättschen/Oberalp, Sedrun under the three RCP scenarios and for three time periods of the 21<sup>st</sup> century. The lines represent the median of all simulations per RCP scenario and 50% of the simulations lie in the shaded ribbon. The horizontal lines indicate the snow reliability at 70% and 90%, respectively, the vertical lines the critical access elevation. At a probability of 1, the lines of the three scenarios overlap



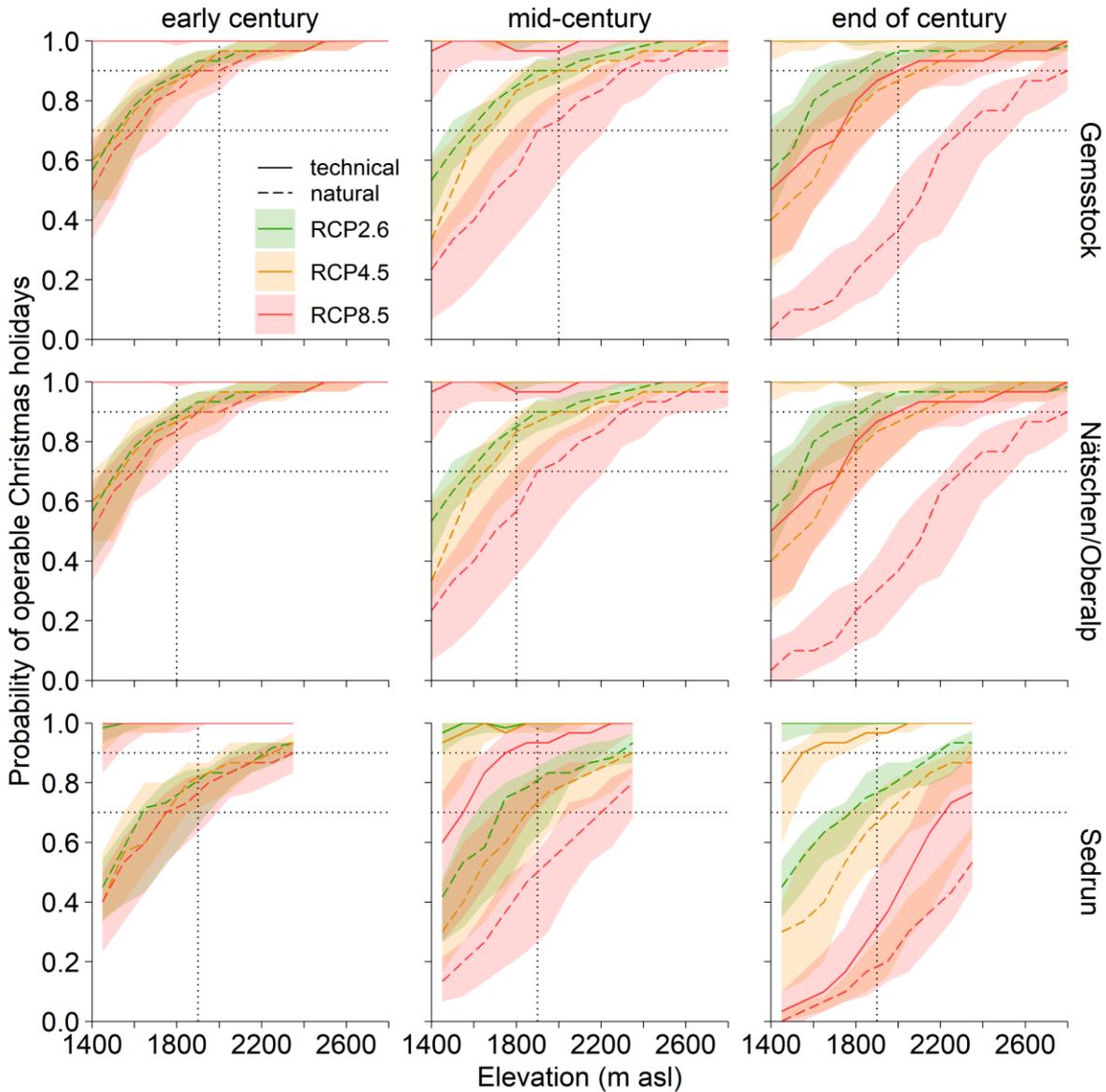
**Figure S4.4** The probability of **100 consecutive days** that are operable for skiing on natural snow (dashed line) and with technical snow (solid line) for the **south**-exposed slopes of the three regions Gemsstock, Nättschen/Oberalp, Sedrun under the three RCP scenarios and for three time periods of the 21<sup>st</sup> century. The lines represent the median of all simulations per RCP scenario and 50% of the simulations lie in the shaded ribbon. The horizontal lines indicate the snow reliability at 70% and 90%, respectively, the vertical lines the critical access elevation. At a probability of 1, the lines of the three scenarios overlap



**Figure S4.5** The probability of 100 operable days with and without snowmaking at the end of the century under RCP8.5. Areas depicted in white are not serviceable for snowmaking and the red line is the critical access elevation



**Figure S4.6** The probability that the resort is operable over the **Christmas holidays** on technical snow (solid line) and with natural snow only (dashed line) for the **north**-exposed slopes of the three regions Gemsstock, Nättschen/Oberalp, Sedrun under the three RCP scenarios and for three time periods of the 21<sup>st</sup> century. The lines represent the median of all simulations per RCP scenario and 50% of the simulations lie in the shaded ribbon. The horizontal lines indicate the snow reliability at 70% and 90%, respectively, the vertical lines the critical access elevation. At a probability of 1, the lines of the three scenarios overlap



**Figure S4.7** The probability that the resort is operable over the **Christmas holidays** on technical snow (solid line) and with natural snow only (dashed line) for the **south**-exposed slopes of the three regions Gemsstock, Nättschen/Oberalp, Sedrun under the three RCP scenarios and for three time periods of the 21<sup>st</sup> century. The lines represent the median of all simulations per RCP scenario and 50% of the simulations lie in the shaded ribbon. The horizontal lines indicate the snow reliability at 70% and 90%, respectively, the vertical lines the critical access elevation. At a probability of 1, the lines of the three scenarios overlap





## Concluding discussion

My PhD thesis with its transdisciplinary addresses multiple consequences of climate change for alpine regions. These comprise the impact of rising temperatures and increased winter precipitation on high-elevation snowmelt dates, including a projection of future snowmelt dates throughout the 21<sup>st</sup> century, which were identified in **chapter 1**. In a unique snow manipulation and summer drought experiment with snow shovelling in late winter/early spring and rainout shelters during the growing season, my co-authors and I created future climatic conditions by shifting snowmelt dates and recurring summer droughts in a late-successional alpine grassland at 2500 m asl. I explored whether photoperiodism hinders the main species of the grassland to profit from earlier snowmelt and longer growing seasons. I therefore examined photoperiod, thermal sums, and the time elapsed since snowmelt as potential drivers of flowering phenology (**chapter 2**). Longer growing seasons could potentially result in increased biomass production, but any benefits may be revoked by recurring summer droughts. Drought may affect plant growth and shift plant allocation patterns, as well limit the nutrient availability and accessibility (**chapter 3**). Besides ecological consequences, a highly evident economic consequence of climate change in alpine regions is the dwindling snow in skiing regions. In **chapter 4**, the future snow reliability for winter sports and tourism (in terms of a snowpack that allows skiing) is projected for the 21<sup>st</sup> century, including estimates for the future water demands for artificial snowmaking.

### *Advancing snowmelt dates at high elevations*

As a result of the work presented in *chapter 1*, I was able to show that the air temperature has a 1.5-fold higher impact on the timing of snowmelt than the mean height of the snowpack. Nevertheless, a higher snowpack height generally delays the snowmelt date, an effect that is less pronounced at higher elevations, where the snowpack already is high. Clearly, the anticipated increase in winter precipitation, which will be falling as snow at high elevations, will not compensate for the rising air temperatures and thus, snowmelt dates will advance at a similar speed at elevations between 1000 and 1500 m asl.

For the period between 1958 and 2019, snowmelt dates advanced by 2.8 days per decade, a trend that was consolidated by a particular advancement in the late 1980s and early 1990s. Because of this strong shift, the magnitude of trends largely depends on the considered time period. Accordingly, Klein et al. (2016) reported that between 1970 and 2015, snowmelt dates advanced almost twice as fast, with 5.8 days per decade.

I found a high linear correlation ( $R^2 = 0.78$ ,  $p < 0.01$ ) of snowmelt dates with the temperature measure  $T_{21d} \geq 5^\circ\text{C}$ . This measure stands for the first day (DOY) when the 3-wk mean of air temperature exceeds  $5^\circ\text{C}$ . Consequentially, snowmelt occurs once the atmosphere has heated up sufficiently. This new metric for the temperature effect on snowmelt is particularly useful for understanding fluctuations of snowmelt dates over longer time periods and/or along elevational gradients. In *chapter 1*, I developed a model to project future snowmelt dates in the Alps based on climate change scenarios for temperature and precipitation. Without a reduction in greenhouse gas emissions, the advancement of snowmelt dates will accelerate to six days per decade by the end of the 21<sup>st</sup> century, with an alpine growing season that will be extended by one month or one third of its current length (RCP8.5). In this context, our experimental snow manipulations achieved a maximum advancement of snowmelt by nine days, which corresponds to a scenario in the early to mid-21<sup>st</sup> century.

*Modulating effect of photoperiod allows species to profit from longer growing seasons*

Short photoperiods and a higher risk for recurring summer droughts may prohibit alpine plant species from profiting of longer growing seasons after early snowmelt (Keller and Körner 2003). The flowering phenology is a rather simple measure for how plants cope with shifts in snowmelt dates. However, the analysis of such phenology data is often not straight forward. The time-to-event analysis adopted in *chapter 2* revealed that four of the seven main plant species of the alpine grassland were highly opportunistic in their flowering behaviour. The main flowering period started after accumulating a species-specific amount of thermal energy (degree hours) or a certain time after snowmelt (days since snowmelt). This group comprised the dominant sedge *Carex curvula*, but also the grass species *Anthoxanthum alpinum* and *Helictotrichon versicolor*, as well as the N<sub>2</sub> fixing forb *Trifolium alpinum*. Even the extraordinary 3-week earlier snowmelt in 2017 in combination with snow removal led to substantially earlier flowering, with no evident restriction through photoperiod. Earlier flowering leaves more time for seed maturation and may therefore enhance plant reproductive fitness. On the other hand, a lacking sensitivity to photoperiod may increase the susceptibility to early frosts and lead to flower abortion. *C. curvula* is a species that starts flowering quickly after snowmelt and therefore it is particularly susceptible. However, this species also features a high spatial dominance and only one out of ten shoots flower each year (Erschbamer et al. 1994) – a strategy which may help to reduce the frost risk. During the field experiment (2016–2018), there was one single frost event with air temperatures down to -3.5 °C in July 2016 (nearby ALPFOR weather station). Overall, earlier snowmelt goes along with an increased frost risk (Inouye 2008), which may reduce the number of flowers, the seed production and the survival of alpine plant species (Kawai and Kudo 2018; Tonin et al. 2019).

The photoperiod sensitive species in my study were the three forbs *Geum montanum*, *Leontodon helveticus*, and *Potentilla aurea*. I showed that after early snowmelt, photoperiodism induced higher thermal sums at the transition to flowering. This modulating effect of photoperiodism allowed these species to slightly protract the transition to flowering after early snowmelt. But snowmelt co-determined the transition to flowering and thus, even the photoperiod sensitive species can partly profit from longer growing seasons. On the other hand, the lower thermal sums accumulated in years with snowmelt around summer solstice indicate an accelerated phenology in years with short growing season. The phenology of these photoperiod sensitive species is well adapted to the large yearly fluctuations in snowmelt dates. With the anticipated earlier snowmelt dates in the future, the increasing delay of flowering will bear an advantage for avoiding early season frosts. For high-elevation and high-latitude plant species, the evidence for photoperiodism so far was mostly restricted to greenhouse studies with fixed daylength treatments (e.g., Heide 2001; Keller and Körner 2003). Here, we supplement this compelling evidence for photoperiodism with *in situ* field data, which further consolidates our understanding of photoperiod as one of the key factors for flowering development at high elevations.

According to the escape strategy (Gugger et al. 2015), some species will advance their flowering under drought, as here observed for the grass *A. alpinum*. The overall effect of the experimentally induced drought on the flowering phenology in the alpine grassland was negligible. However, drought may impair seed maturation and therefore reduce the reproductive success of alpine plant species (Galen 2000).

*Drought increases the allocation of biomass to below-ground*

Neither earlier nor later snowmelt affected the above- or below-ground biomass production. As such, late successional grasslands do not seem to benefit from longer growing seasons in terms of

production. However, after 10.5 weeks of rain exclusion with rainout shelters, I observed a clear reduction in above-ground biomass formation. In line with the functional growth analysis (Körner 2014), there was a shift towards below-ground biomass allocation under drought, as previously also observed in drought experiments at lower elevations (e.g., Kahmen et al. 2005; Gilgen and Buchmann 2009). However, the overall response depended on the duration and intensity of the drought. Rain exclusion for the first half of the growing season had no effect on the above-ground phyto- and biomass production, but strongly enhanced the below-ground production (+19%; in-growth cores), resulting in an overall increase of the yield. In contrast, rain exclusion for almost the entire growing season reduced the above-ground production (-16% phytomass, -19% biomass) but remained without effect on the below-ground production, inducing an overall decrease in the community biomass. In a prior 6- and 12-wk drought experiment in the same region, Schmid (2017) observed increases in the below-ground biomass (+47 to +50%) and reductions in the above-ground biomass (-12 to -35%). However, the soil water content on the steep slopes (40° inclination) was constantly higher than in our experiment. The author highlighted that increases in the below-ground biomass and reductions in above-ground phytomass go along with a lower plant cover, most likely facilitating soil erosion. These results and the low above-ground biomass production (-20%) in the naturally dry year 2018 strongly underline the high relevance of the timing and intensity of droughts for alpine grassland.

#### *Nutrient uptake of *C. curvula* was unhindered by drought*

One of the main hypotheses of my thesis was that drought would primarily limit the nutrient availability and accessibility in the drying topsoil of the grassland. However, our field experiment with snow manipulations and summer drought revealed that most of the mass loss of on-site litter occurred over the nine winter months (37.1%), whereas there was no further mass loss over the subsequent growing season, independently of the litter type. The decomposition was only slowed down when on-site litter was provided at the start of the growing season, not before the winter months. Thus, drought did not significantly affect the provision of nutrients though a reduced decomposition in the topsoil. An additional nutrient layer placed in the root-free in-growth cores revealed that the nutrient induced increase in the root mass was lower under drought, even though this effect was not statistically significant. Nevertheless, by means of maize litter that was enriched in <sup>15</sup>N, we could also show that nitrogen uptake of *C. curvula* was unhindered by drought, even in combination with early snowmelt dates. Due to its high spatial dominance, *C. curvula* is presumably a good competitor for soil nutrients. So far, these results are restricted to nitrogen uptake of *C. curvula*. In the future, soil cores could reveal patterns of nutrient allocation under drought, allowing further conclusions about the impact of climate change on the nutrient cycle of alpine grasslands.

#### *Increased water consumption calls for new water management strategies*

Our in-depth analysis of the ski resort *Andermatt-Sedrun-Disentis* revealed an overall high resilience against climatic changes throughout the 21<sup>st</sup> century. This is mainly due to the recently installed snowmaking facilities and the multiple access points of the resort, but also due to the generally high natural snow reliability. Under a climate change scenario with unabated emissions, it is likely that in the mid-term (ca. 2050), the resort will profit because lower-elevation resorts are going out of business. However, over the whole century, the resort will anticipate economic losses, particularly over the currently profitable Christmas holidays. Moreover, the expenses for snowmaking will rise considerably, as the water consumption will increase by 23% in the mid-21<sup>st</sup>

century, and by 79% by the end of the century (RCP8.5). Although the increase in water consumption is substantial, the international comparison shows that it is lower than in most ski areas (see Steiger et al. 2019). For the mid-century, increases in water consumption will rise by 46% to 80% in China (Fang et al. 2019), by 45% to 65% in Austria (Steiger and Scott 2020), and by 12% to 86% in the US (Jones et al. 2008), highlighting the high snow reliability of *Andermatt-Sedrun-Disentis*.

Even though the Alps are often referred to as the water tower of Europe, water can get restrictive when competition amongst stakeholders arises. In Switzerland, when stakeholders are confronted with water deficits it is commonly not a consequence of an actual water shortage, but of inefficient water management strategies (Clivaz and Reynard 2008; Schneider et al. 2016). For alpine communities such as Andermatt, Sedrun and Disentis, it is therefore important to develop water management strategies that incorporate the future availability, and the future water needs of the various stakeholders in the region.

### Conclusions

Snowmelt in the alpine vegetation zone will increasingly occur earlier in the season, which will prolong the alpine growing season substantially. Photoperiodism will primarily slow down the plant development after early snowmelt followed by low temperatures, but it will not completely prohibit the plant's sprouting after early snowmelt. For my field site, I anticipate that snowmelt will occur one month earlier by the end of the 21<sup>st</sup> century. However, the year 2017 with three weeks earlier snowmelt clearly demonstrated the large inter-annual variability of snowmelt dates. Such a particular year at the end of the century may lead to a 2-month earlier snowmelt than today's average, and photoperiod restrictions will then play an important role for avoiding frost. However, in an average year by the end of the century (1-month earlier snowmelt), as studied here in 2017 with additional snow removal, will allow the opportunistic plant species of this alpine grasslands to profit from longer growing seasons and may increase their reproductive success in years without early season frosts. However, the earlier start of the growing season will not allow for enhanced biomass production. Recurring summer droughts may cause an increased biomass allocation to below-ground plant organs, but overall reductions in biomass are only expected when droughts span the majority of the growing season. At least for the dominant sedge *C. curvula* the availability and accessibility of nutrients will be provided even under severe drought, as high foliar  $\delta^{15}\text{N}$  (26.5‰) revealed the successful nutrient uptake of the sedge. However, it remains unclear whether this is also true for the other plant species in this grassland. The successful root foraging of *C. curvula* for nutrients even under drought may cause shifts in the plant species composition in the longer term.

Overall, late successional alpine grassland with clone ages of *C. curvula* of up to 4200 years (De Witte et al. 2012) is highly resilient against future climatic changes with earlier snowmelt and recurring summer droughts. This conclusion bases on observations of three years with snow manipulations, two of which were combined with summer droughts.

A more direct impact of climate change in alpine regions is on the skiing industry. As most of the larger high-elevation ski resorts of the alpine arc, *Andermatt-Sedrun-Disentis* is well equipped to mitigate snow scarce winters by means of snowmaking. The increased water consumption caused by ski resorts and other stakeholders calls for an overarching water management strategy that incorporates the future development of water usage.

## References

- Clivaz C, Reynard E (2008) Crans-Montana: Water resources management in an alpine tourist resort. In: Beniston M, Allen-Diaz B, Bradley RS, et al. (eds) *Mountains: Sources of water, sources of knowledge*. Springer, Dordrecht, p 386
- De Witte LC, Armbruster GFJ, Gielly L, Taberlet P, Stöcklin J (2012) AFLP markers reveal high clonal diversity and extreme longevity in four key arctic-alpine species. *Mol Ecol* 21:1081–1097. doi: 10.1111/j.1365-294X.2011.05326.x
- Erschbamer B, Winkler J, Wagner J (1994) The vegetative and generative development of three *Carex curvula* in the Central Alps. *Flora* 189:277–286
- Fang Y, Scott D, Steiger R (2019) The impact of climate change on ski resorts in China. *Int J Biometeorol*. <https://doi.org/10.1007/s00484-019-01822-x>
- Galen C (2000) High and dry: drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum* (*Polemoniaceae*). *Am Nat* 156:72–83. doi: 10.2307/3079032
- Gilgen AK, Buchmann N (2009) Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. *Biogeosciences* 6:2525–2539. doi: 10.5194/bg-6-2525-2009
- Gugger S, Kesselring H, Stöcklin J, Hamann E (2015) Lower plasticity exhibited by high- versus mid-elevation species in their phenological responses to manipulated temperature and drought. *Ann Bot* 116:953–962. doi: 10.1093/aob/mcv155
- Heide OM (2001) Photoperiodic control of dormancy in *Sedum telephium* and some other herbaceous perennial plants. *Physiol Plant* 113:332–337. doi: 10.1034/j.1399-3054.2001.1130305.x
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362. doi: 10.1890/06-2128.1
- Jones B, Scott D, Dawson J (2008) Climate change vulnerability of the US Northeast winter recreation–tourism sector. *Mitig Adapt Strateg Glob Chang* 13:577–596. doi: 10.1007/s11027-007-9136-z
- Kahmen A, Perner J, Buchmann N (2005) Diversity-dependent productivity in semi-natural grasslands following climate perturbations. *Funct Ecol* 19:594–601. doi: 10.1111/j.1365
- Kawai Y, Kudo G (2018) Variations in ramet performance and the dynamics of an alpine evergreen herb, *Gentiana nipponica*, in different snowmelt conditions. *Am J Bot* 105:1813–1823. doi: 10.1002/ajb2.1186
- Keller F, Körner C (2003) The role of photoperiodism in alpine plant development. *Arctic, Antarct Alp Res* 35:361–368. doi: 10.1657/1523-0430(2003)035[0361:TROPJA]2.0.CO;2
- Klein G, Vitasse Y, Rixen C, Marty C, Rebetez M (2016) Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than later snow onset. *Clim Change* 139:637–649. doi: 10.1007/s10584-016-1806-y
- Körner C (2014) Ökologie. In: Kadereit JW, Körner C, Kost B, Sonnewald U (eds) *Strasburger Lehrbuch der Pflanzenwissenschaften*. Springer, Berlin Heidelberg, pp 740–810
- Schmid S (2017) Impacts of climate change on alpine grassland ecosystems: Responses in structure and function. Dissertation. ETH Zürich. p 170
- Schneider F, Bonriposi M, Graefe O, Herweg K, Homewood C, Huss M, Kauzlaric M, Liniger H, Rey E, Reynard E, Rist S, Schädler B, Weingartner R (2016) MontanAqua: Tackling water stress in the Alps. Water management options in the Crans-Montana-Sierre regions (Valais). *GAIA* 25/3:191–193
- Steiger R, Scott D (2020) Ski tourism in a warmer world: Increased adaptation and regional economic impacts in Austria. *Tour Manag* 77:104032. doi: 10.1016/j.tourman.2019.104032
- Steiger R, Scott D, Abegg B, Pons M, Aall C (2019) A critical review of climate change risk for ski tourism. *Curr Issues Tour* 22:1343–1379. doi: 10.1080/13683500.2017.1410110
- Tonin R, Gerdol R, Tomaselli M, Petraglia A, Carbognani M, Wellstein C (2019) Intraspecific functional trait response to advanced snowmelt suggests increase of growth potential but decrease of seed production in snowbed plant species. *Front Plant Sci* 10:1–12. doi: 10.3389/fpls.2019.00289

