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Simple field-based surveys reveal climate-related anomalies in mountain grassland production

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ABSTRACT

Sensitivity of grassland biomass production to climate is critical to impacts on multiple ecological processes and ecosystem services. Understanding its climate determinants is essential for climate change adaptation. This requires long-term monitoring, using robust methods that are appropriated by stakeholders. We tested the sensitivity of easily measured sward height to interannual climate variation in mountain grasslands. Using twelve consecutive years of measurements across 67 grassland plots representative of six land-use types associated with different landscape positions, we show that peak green biomass increased with mean summer months (June and July) maximum temperature. Different land-use types responded to specific combinations of climate parameters, but all except higher-elevation summer pastures were sensitive to summer months temperatures. We did not detect any effects of drought, with summer precipitation instead decreasing peak biomass of some grasslands due to cooling and cloudiness, also suggesting that soil water recharge from snowmelt was enough to sustain the first growth cycle. Summer pasture peak biomass decreased with number of frosts during the onset of growth in May. These result support the robustness and sensitivity of sward height as an indicator for climate response of peak fodder biomass. Differential responses across land-use types suggest some resource complementarity which can support tactical adaptation for farmers. During the three recent hottest summers (2015, 2017 and 2018) production was well below predicted values from actual temperatures, suggesting a potential regime shift when the vegetative growth period is shortened by temperature-driven acceleration in phenology and/or heat stress combined with high light intensity causing physiological damage. The baseline regime and the anomalies in hottest years need confirmation for longer time series and across a greater geographic extent. Further effects of drought and of an extended growing season are also likely for post-harvest or grazing regrowth.

1. Introduction

Grasslands are a critical asset in mountains, where they provide multiple benefits to societies and support large biological and cultural diversity (Körner et al., 2005). In the European Alpine Space they cover 18% of the total area and supply an estimated average of 44.8 M tons of dry matter per hectare and per year, supporting livestock for dairy and meat production (Jäger, 2017; Schirpke et al., 2019). Fodder production is however highly variable both spatially and temporally (Choler, 2015; Corona-Lozada et al., 2019; Jonas et al., 2008; Schirpke et al., 2019). In particular, effects of interannual climate variability, extreme events and trend change on fodder production will have considerable consequences on the futures of mountain agriculture and landscapes (Darnhofer, 2014; Nettier et al., 2017; Sautier et al., 2013).

Biomass production from temperate grasslands is controlled for a given composition and management by incident radiation, temperature, soil moisture (determined by the balance between precipitation and evapotranspiration for a given soil) and available nutrients (Duru et al., 2010a; Fraser, 2018). In cold biomes like mountains, snow cover duration is also critical for determining grassland production potential through vegetation composition (Carlson et al., 2015; Carlson et al., 2017; Liu et al., 2018a), and through interannual variability of production (Choler, 2015; Jonas et al., 2008; Liu et al., 2019). Studies at national to continental scales have linked inter-annual variations of grassland production to simple meteorological variables (temperature, precipitation) at varying time resolutions (e.g. monthly or sub-monthly means) (reviewed by (Fraser, 2018)). Further composite variables such as growing degree days (the sum of positive mean daily temperatures until harvest or specific phenological states), potential evapotranspiration and its difference with precipitation, or number of frost

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days have also been used for modelling observed variations (Choler, 2015; Corona-Lozada et al., 2019; Jonas et al., 2008) and for mechanistic models of production (Calanca et al., 2016; Duru et al., 2010a).

The understanding of climate responses of grassland biomass production is supported by combinations of observations, experiments and modelling (Fraser, 2018). Long-term monitoring offers a unique opportunity for detecting response patterns, parameterising and testing models (Rogora et al., 2018; Trnka et al., 2006). Low-cost monitoring is also a means to empower stakeholders by implicating them in data collection, interpretation and communication (Dobremez et al., 2014; Reed et al., 2008). For this, robust indicators and methods that can be appropriated by stakeholders are needed. Such indicators should be relatively simple and thus rapid, robust and sensitive to the driver of interest, here climate (Feld et al., 2009). Sward height is a commonly used indicator of biomass production in ecological and agronomic studies (Marriott et al., 2004; Oliveras et al., 2014; Stewart et al., 2001). Accordingly, community mean plant vegetative height is a strong predictor of upland grassland production and its response to management (Lavorel et al., 2011; Pakeman, 2011). Sward height is also regaining current interest given new imaging technologies that can capture fine-scale variations in grassland physical properties that can be linked to production and other ecosystem services (Forsmoo et al., 2018).

In this study we tested sward height as a method for monitoring mountain grassland production, with the objective that it should be useable for long-term monitoring by non-specialists (e.g. staff from protected areas, agricultural extension officers…). This paper first presents the sward height-based field measurement method. We then test the robustness and sensitivity of this indicator by analysing a twelve-year time series representing a credible range of climate and productivity variation in the Central French Alps, for data collected across a set of 67 grassland plots from the main vegetation types across the Oisans/Briançonnais region (Jouglet, 1999). Finally, we highlight how a potential tipping point in fodder production can be detected for recent summer temperature extremes. We conclude that desired criteria for an indicator of forage production response to climate variation are met and discuss possible extensions and improvements.

2. Materials and methods

2.1. Field site

Plant biomass data was collected from a set of 67 grassland plots managed by farmers at the Lautaret study site (45°03′N, 6°24′E). The site is located in the Central French Alps on the south-facing slopes of Villar d'Arène and covers 13 km^2 with elevation ranging from1552 to 2442 m a.s.l. (a detailed site description can be found in (Quétier et al., 2007)). It is managed by low- to medium intensity livestock rearing, involving a variable combination of organic fertilization at low doses (eight tons of manure per hectare every 2–3 years), mowing and grazing at low intensity (< 2 days of livestock units per hectare per year). In total, six land-use types form a vegetation mosaic: three on previously cultivated terraces (currently fertilized and mown (TFM), mown but not fertilized (TM), or unmown and grazed in spring and autumn (TU)), two on permanent grasslands with no history of cultivation and a multi-century history of mowing (currently mown (UM), unmown and summer-grazed (UU), and one on never mown summer grasslands (> 2000 m) (SP). Average production at peak biomass (July) ranges from 2.5 to 5.5 tDM.ha^{-1}.yr^{-1} (Jouglet, 1999; Lavorel et al., 2011).

The climate is subalpine with a strong continental influence due to a rain shadow with respect to dominant westerly winds. Mean annual precipitation is 956 mm at the nearest Météo France climate station (Besse-en-Oisans, station number 38040001, Lat 6°10′18″E Long 45°04′12″N, Altitude 1525 m) and the altitude-adjusted mean monthly temperatures are −4.6 °C in January to 11 °C in July (at 2050 m a.s.l.). Snow disappears from the study area between late March (at 1700 m) and mid- to late-May (at 2100 m). Regional mean temperatures have increased by 0.3 °C per decade since the beginning of the 20th century with a greater increase (0.4–0.5 °C) in summer than in winter (0.1 °C) or autumn (0.2 °C) (GREC-Sud, 2018). Total annual precipitation is stable to slightly decreasing for 1959–2015, with a weak increase in spring precipitation. Overall the precipitation signal remains uncertain, as are precipitation projections. Interannual climate variability is marked and has increased since 2000 (Beniston, 2015; Durand et al., 2009b), including recurrence of heat waves (Corona-Lozada et al., 2019).

2.2. Measuring standing biomass using sward height as an estimator

2.2.1. Reference biomass measurements

In the years 2007–2010 biomass estimates were carried out in a subset of twenty four representative 100 m^2 grassland plots using calibrated visual estimations of standing biomass (Redjadj et al., 2012). In each plot, two operators made visual estimates of total (green biomass and litter) and green dry biomass in twelve independent randomly located 50x50 cm quadrats (i.e. 24 quadrats per plot across the two operators) each. These 24 quadrats were harvested manually to ground level, pooled and sorted to green and dead biomass, dried and weighed. For each operator during each year a calibration regression equation was then established between the operator's mean visual estimate of biomass per ha and the sampled standing and green biomass per ha. We note that this calibration was across plots and not at quadrat-level because individual quadrat visual estimates are not considered as meaningful on their own as opposed to plot averages (Tothill et al., 1992). The calibration equation was then used to correct the visual estimates in those quadrats in which actual biomass was not harvested (Suppl. Mat. A). Estimated biomass values for the 12 quadrats in each plot were averaged to give a mean total and green biomass per plot in t/ha per plot.

2.2.2. Relationship between reference biomass measurements and measures of sward height

Concurrently with these calibrated visual estimates of total and green biomass, sward height measurements were also taken within at least each of the 24 plots (total numbers 2007: 27, 2008: 41, 2009: 25, 2010: 26). Such measures of table or canopy closure height have been previously used in grasslands to successfully provide estimates of standing biomass (Redjadj et al., 2012; Stewart et al., 2001) and have been shown to reliably reflect spatial variations in biomass production across Swiss mountain grasslands (Jonas et al., 2008). Sward height measurements involved measuring 60–80 replicates of the height at which vegetation in the plot began to form a closed canopy (otherwise called table height). Measurements were averaged to give a mean sward height per plot. Measurements for the total of 119 plots across the four years (2007–2010) showed a highly significant relationship between vegetation sward height and biomass (R^2 = 0.689 for total biomass, and 0.701 for green biomass), and no significant difference in this relationship between years (Suppl. Mat. A). Considering the six land-use types individually, while there was overall a highly significant relationship between sward height and biomass (R^2 = 0.697), and there was no significant difference in this relationship between land-use types (Suppl. Mat. A).

2.2.3. Validated method for using sward height to estimate total and green biomass

Given the lack of significant differences across land-use types in the relationships between green biomass and sward height, data from all types and over the four years of measurements was pooled and a simple regression equation established explaining a high proportion of the variance between these two parameters (R^2 = 67%, $p < 0.001$) (Fig. 1). Measurements of biomass from 2010 onwards were carried out using only sward height measurements converted to green biomass

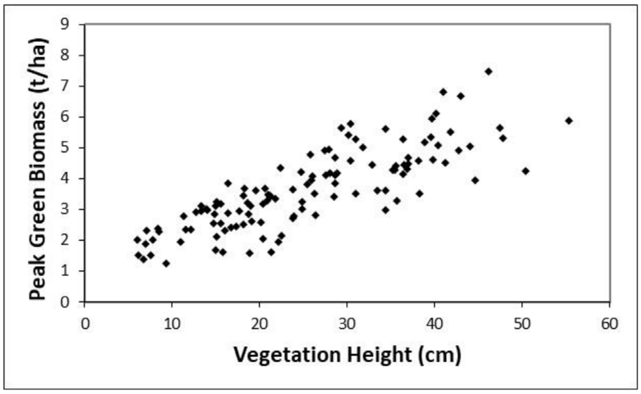


Fig. 1. Reference calibration between peak green biomass and vegetation height (2007–2010).

using the following equation: Green Biomass (t DM/ha) = (0.0938 * sward height (cm)) + 1.2616

2.3. Biomass data set

The data set consisted of such estimated biomass records from 2007 to 2018, representing 12 time-correlated replicates. Mean green biomass was determined in 2–24 plots from each of six land-use types (TFM, TM, TU, UM, UU, SP) per year (due to plots being missed due to grazing/mowing, vole damage etc.), giving a total of 649 samples over the time course of the study, with 35–67 plots measured each year (Details in Suppl. Table B1). The plots in which this time-series biomass data was taken were the same as those in which the calibration equation was developed.

2.4. Climate data set

Climate data (daily minimum and maximum temperatures; precipitation) was obtained for 2007 to 2018 from the Météo France weather station at Besse-en-Oisans (Station number 38040001, Lat 6°10′18″E Long 45°04′12″N, Altitude 1525 m) (Fig. 2). This was the nearest complete station to the Lautaret field site and was assumed to provide an acceptable proxy for yearly climate variation. A temperature correction of + 0.6 °C per 100 m altitudinal gain was applied (Theau and Zerourou, 2006) to inter-calibrate the station of Besse-en-Oisans (Altitude 1525 m) and a second station at Villar d'Arène Pied du Col (altitude 1665 m), and validated using a regression analysis over the 2007 growing season (1 April – 31 July; R^2 = 0.662, n = 122). A further validation of Besse-en-Oisans as a reference station was made by a regression analysis between the Villar d'Arène meteorological station data for 2008 and records by two Hobo Onset® stations at the Les Cours locality (altitude 1810 m) and at the Lautaret alpine botanical garden (altitude 2070 m). Mean temperatures over the study period were ~ 2 °C higher than the long term mean, with mean minimum monthly temperatures tracking most closely the long term average (Fig. 2). There was a 2–3 °C increase in spring and summer as compared to long term mean, while autumn and winter temperatures were less different. Mean precipitation was overall similar to the long-term average. A Principal Component Analysis of interannual variation across the study period is presented in Suppl. Mat. Fig. C1.

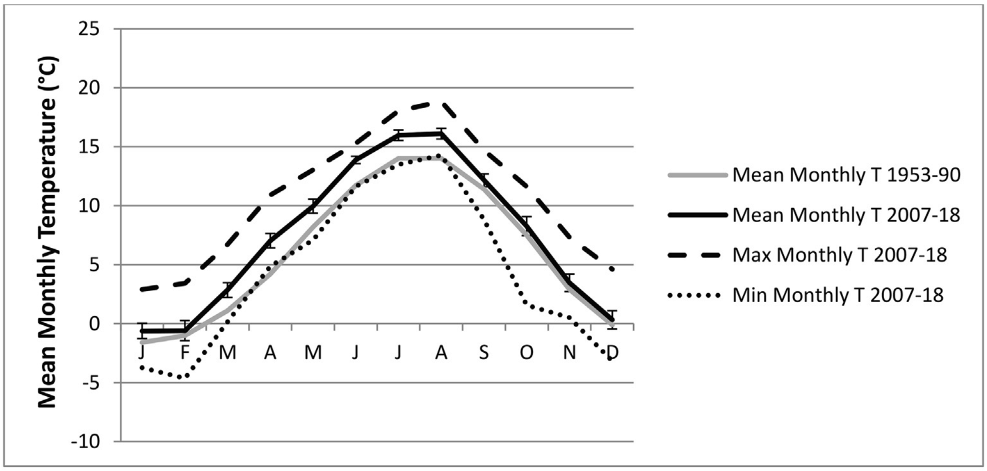
Synthetic climate variables were calculated in order to capture relevant agrometeorological parameters (Choler, 2015; Nettier, 2016). The cumulated growing degree days (GDD) over a time window is an indicator of cumulated energy for growth, and known to affect phenology of common grassland species (Ansquer et al., 2009). The cumulated number of frost events over the time window (FST; TN < 0 °C) represents risks of damage to growing tissues, especially at the beginning of the season. Mean monthly soil moisture (MSMT) was estimated using the Thornthwaite monthly water balance model (Garnier et al., 2007; Thornthwaite and Mather, 1955). A remote sensing estimate of the date of snowmelt each year at site level was added as a proxy for of the date of onset of the growing season. Chosen climatic explanatory variables thus encompassed a range of known potential climatic drivers of differences in biomass production in alpine herbaceous vegetation, including variables capturing temperature, soil moisture, frost and growing period length (snow free period), and this over time windows relevant to determining plant growth and biomass development in a sub-alpine environment (Choler, 2015; Jonas et al., 2008). Each variable was calculated for differing time windows of each year so as to isolate parts of the growth period considered *a priori* most important in determining plant growth and biomass development. Suppl. Mat. C presents full list of calculated parameters (Table C1), with an explanation of the calculation methods and definition of the various time windows. Initial analyses using climate variables calculated over the whole year, or for the full seasons of Winter (Dec, Jan, Feb), Summer (June, July, August) or Autumn (Sep, Oct, Nov) showed no significant correlations with the biomass variables, and thus were not included in the final analyses. Likewise, an exploration of the relevance of decadal rather than monthly resolution for explanatory climate variables showed no improvement on statistical models, hence with operationality for users we kept the monthly resolution.

2.5. Analysis of correlations between differences in biomass production and the climatic variables

For the correlations with climate variables, as all of the same plots were not necessarily measured every year, and most of all because there was only one climate measure common to all plots each year, it was not possible to use individual plots as independent data points. For each land-use type the mean biomass of all plots measured in a given year was calculated, and then these values averaged across the 11 years from 2007 to 2017 to give a mean biomass per land-use type over the time course of the survey. 2018 was only incorporated in final model validation (see below). Mean biomass per land-use type for the whole time period was then subtracted from the mean biomass per land-use type of each year, to give the biomass production anomaly from the overall mean for each year. Thus the biomass data used in the climate correlations consisted of a value of the mean biomass anomalies from the 11-year average mean biomass per trajectory per year (thus 11 annual data points per land-use type). Two other biomass variables were also calculated: mean biomass anomaly per year for grasslands other than summer pastures (TFM, TM, TU, UU and UM combined; all < 2000 m), and the mean biomass anomaly per year for all types combined.

The data set thus comprised of series of 8 response variables (the biomass anomalies per year for the six land-use types, plus the two combined biomass anomalies), and a series of 40 explanatory variables, over the 11 years of measurement. To determine what part of the variation in anomalies in biomass production between years could be attributed to climatic effects, and which climate variables were explanatory, we used linear regression with correlated errors using REML estimation (Genstat 16th edition). This method can be used to fit regression models to data such as repeated measurements. Where required data was transformed to meet assumptions of normality. For each biomass response variable we initially carried out a simple regression with each explanatory climate variable in order to select relevant variables (Suppl. Table 1). Those climate variables which had a significant correlation with biomass anomalies were retained and ranked in order of their degree of variance explained. Subsequently, multiple regression models for each of the biomass anomaly variables were developed by fitting those climate variables significant on their own in a stepwise regression manner, adding variables in the order of their degree of variance explained singly. Added variables were retained, or discarded on the basis of their significance in the presence of

A.



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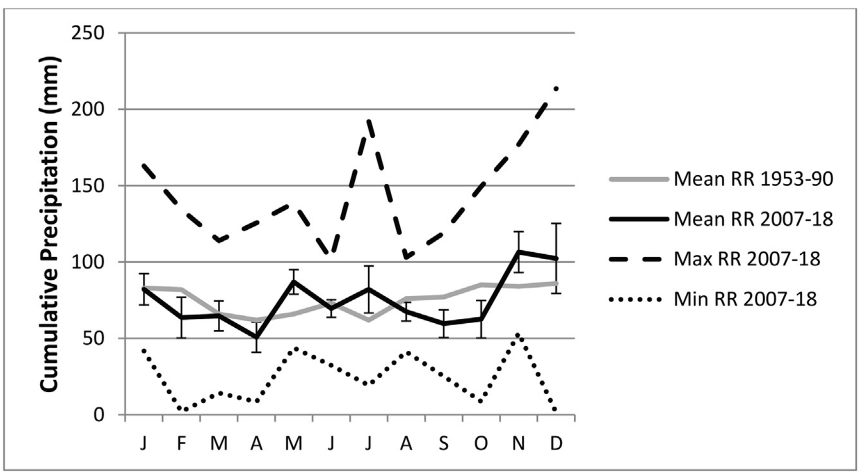

Fig. 2. **A**. Mean, maximum and minimum monthly temperatures at Besse-en-Oisans over the study period as compared to the long term mean monthly temperatures (1953–90). **B**. Mean, maximum and minimum monthly precipitation over the study period at Besse-en-Oisans as compared to long term mean monthly precipitation (1953–90).

other, more significant variables, until a final most parsimonious model on the basis of compared Aikake criterion values was retained which included only significant climate variables and which maximized the total variance explained.

In order to synthesise effects and their variations across land-use types a co-inertia analysis of the biomass variation over time amongst the land-use types (mean biomass anomaly each year by type) with the climate variation over time (a selection of climate variables identified as being significant in the regression analyses) was carried out using the *ade4* R-package software (Dray and Dufour, 2007).

3. Results

3.1. Interannual variability in peak biomass

Mean peak biomass production varied from an average of 1.5 – 3.25 t/ha (kg/m^2) for summer pastures (SP) and grazed terraces (TU), to 4.1 – 6.6 t/ha (kg/m^2) for fertilized hay meadows on terraces (TFM) (Fig. 3). Coefficients of variation were greatest for TFM (44%) and UM (31%) and smallest for TM (21%) (Suppl. Mat. B, Fig. B2).

3.2. Response of biomass production anomalies to climate variables

In the following we first report the explanatory power of statistical models of inter-annual variation in peak biomass and the relative contributions of different significant variables for successive analyses of the complete data set (all plots), all land-use types except summer pastures (due to their qualitatively different response) and individual land-use types. A first highly explanatory model was developed for years until 2014, and is henceforth considered as the baseline period. Inclusion of summer months (June-July) for subsequent years, including the three warmest years on record (2015, 2017, 2018) resulted in no significant models being found. The final models retained for the baseline period (Table 1) revealed the strong effects of air temperatures during the period of maximum plant growth (June-July) in determining peak biomass. Mean maximum temperatures during the period of maximum plant growth (June-JulyTX) explained 61.5% of inter-annual variance across all plots, as compared to 49.1% for growing degree days for the same period (June-JulyGDD) (Suppl. Table 1). When excluding summer pastures, mean maximum temperatures during July (JulyTX) explained 60.6% of inter-annual variance, as compared to 49.1% for growing degree days for the same period (July GDD). The final best fit multi-linear models explained high amounts of variation in the biomass production, with mean minimum temperature across the growth period

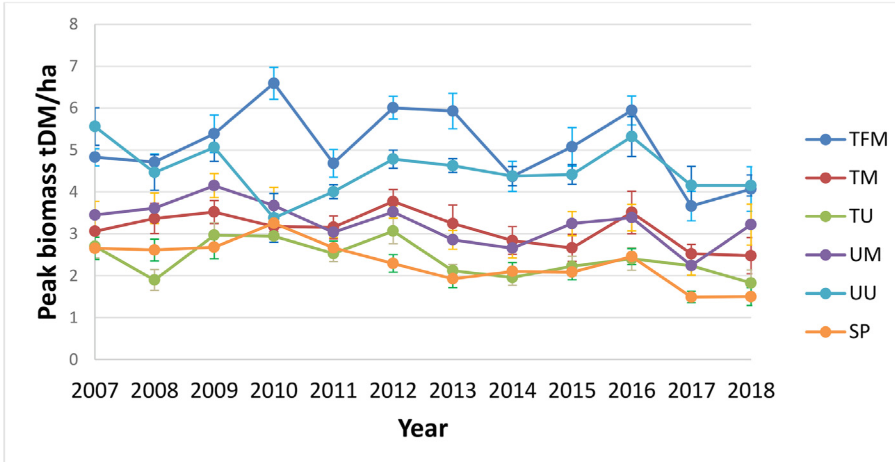

Fig. 3. Time series of mean peak biomass across land-use types. Error bars represent variation across plots for a given land-use type.

and July precipitation explaining 89% of inter-annual variance across all plots. In models for individual land-use types the percentage of variance explained ranged from 36% (UU) to 92% (TFM), and reached 86% for grasslands other than summer pastures.

Secondly, we detail the effects of significant climate variables. In the analysis considering land-use types other than summer pastures, there was a significant positive effect on peak biomass of increasing temperatures (TN or TX) over the growth period until peak biomass and especially in June-July, the most active plant growth period (Fig. 4, Suppl. Fig. 1). Statistical models for individual land-use types retained either mean minimum (TFM, TM, grasslands other than summer pastures) or mean maximum (TM, TU, UM, UU) temperatures (Table 1). Growing degree days were never retained in final models given their less explanatory effects than temperature variables (Suppl. Table 1), although for TFM a model including JulyGDD was nearly as explanatory as the final model with mean minimum temperatures (Table 1). We also observed that increase in precipitation during this same growth period was a weak predictor of decreases in peak biomass in TFM and TU. This effect is most likely due to significant correlations (R^2 = 0.453, p = 0.047 for Spring TX vs Spring RR during the baseline period) between increasing precipitation and cooler low-radiation conditions (Suppl. Mat. C Fig. C2), resulting in decreasing plant growth and biomass production beyond lower temperatures effects. Increasing frosts during May significantly reduced peak biomass in UM and especially SP located at higher altitude.

3.3. Co-inertia analysis

The co-inertia analysis of the biomass variation over time amongst land-use types (mean biomass anomaly each year by land-use type) with the variation over time of significant climate variables showed consistent patterns with the regressions. The RV-coefficient showed a highly significant correlation of 0.744 between the two analyzed tables (Monte-Carlo test based on 999 replicates, simulated p-value: 0.002). The first eigenvalue of the co-inertia analysis explained 85.8% of the total explained variance between the two datasets, showing primary relevance of the links between biomass variation and the climate parameters along this first axis.

This analysis emphasized the positive associations revealed by the univariate analyses between peak biomass anomalies (especially in types TFM, TM, TU and UM) with growth period and June-July mean maximum temperatures, and the negative association of anomalies with increasing accumulated precipitation over the growth period or June-July (Fig. 5). Also, the analysis singled out the response of summer pastures whose negative biomass anomalies were primarily determined by May frosts. Note also the lack of responsiveness of unmown and

Table 1
Climate variables retained within the multiple regression models explaining peak biomass variation for each of the land-use types. For each of them the % variation explained by the retained climate variables, the significance (P) of the full model, the significance of the effect of each retained climate variable and the direction and magnitude of the standardised effect for each of the retained climate variables are presented. TN: mean minimum temperature, TX: mean maximum temperature, RR: cumulated precipitation, FST: number of frosts, GrthPrd: growth period, SMST: soil moisture index.

Biomass anomaly response variable	Retained climate variables	% variation explained by full model	Full model p	Effects p	Standard.Effect
TFM(TN model)	JulyTN	91.6	< 0.001	0.005	0.4140
	JulyRR			0.043	−0.00743
TFM(GDD model)	JulyGDD	90.1	< 0.001	0.009	0.01165
	JulyRR			0.039	−0.00592
TM(TN model)	GrthPrdTN	45.8	0.027	0.027	0.444
TM(TX model)	GrthPrdTX	37.7	0.046	0.046	0.2176
TU	GrthPrdTX	68.5	0.013	0.044	0.270
	JuneJulyRR			0.035	−0.00537
UM	JuneJulyTX	79.7	0.004	0.002	0.2974
	MayFST			0.016	−0.0764
UU	GrthPrdTX	35.6	0.053	0.053	0.474
SP	MayFST	42.1	0.035	0.035	−0.0870
T1-5 (Simple model)	JulyTX	60.6	0.008	0.008	0.1457
T1-5 (Complex model)	GrthPrdTN	85.7	0.001	0.013	0.412
	JulySMST			0.003	−0.00881
All (Simple model)	JuneJulyTX	61.5	0.008	0.008	0.2400
All(Complex model)	GrthPrdTN	89.2	< 0.001	0.052	0.2251
	JulyRR			0.001	−0.005570

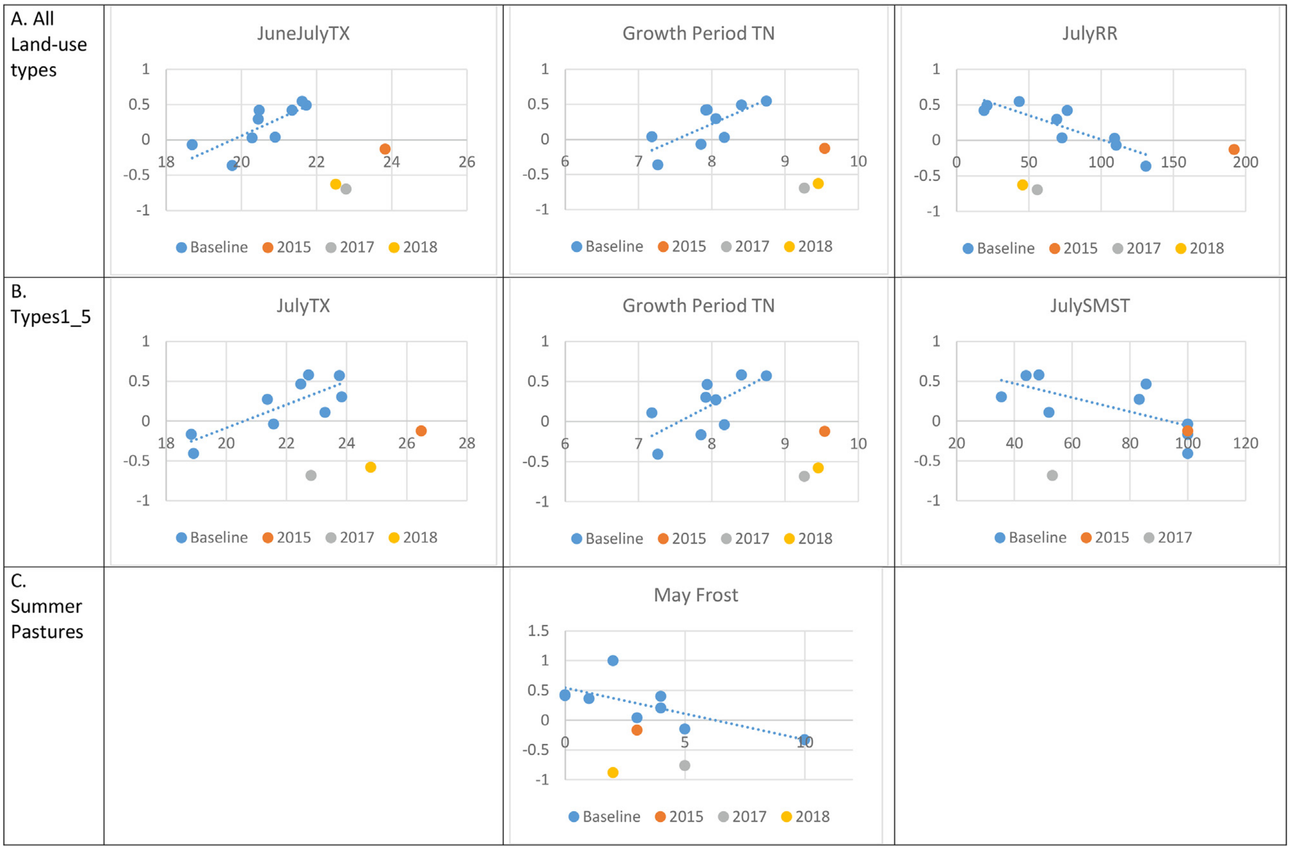

Fig. 4. Relationships between peak biomass and significant explanatory variables for A. All land-use types, B. All grasslands except summer pastures, C. Summer pastures. Each graph presents data with significant regression for the baseline regime (2007–2014 + 2016) and additional points for heat extremes of 2015, 2017 and 2018. The full set of relationships for individual land-use types is presented in Supplementary Fig. 1.

summer-grazed (UU) grasslands to analysed variables, consistent with univariate analyses (Suppl. Table 1).

3.4. Anomalies in the hottest summers

We failed to find any significant model when inserting one or all of the following years: 2015, 2017 and 2018, which were the hottest summers within our time series (mean June-July TX of 23.8, 22.8 and 22.5 °C respectively). Their deviation from the baseline relationships with temperature could therefore not be captured by any of the available variables. Adding them as supplementary points in the baseline regression models (Fig. 4, Suppl. Fig. 1 for complete results) shows that

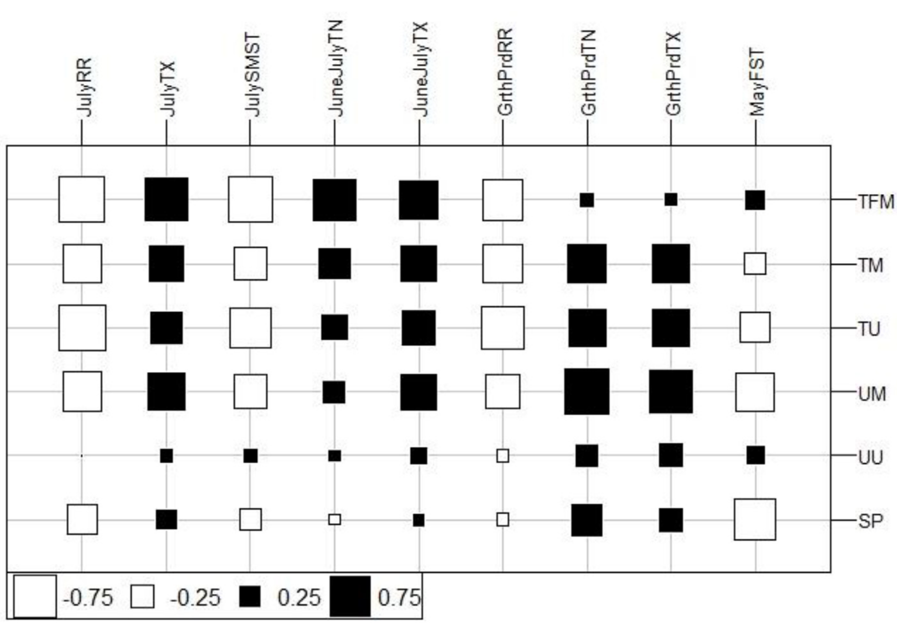

Fig. 5. Correlations between selected climate variables (vertical) and peak biomass anomalies across land-use types (horizontal) from co-inertia analysis.

for the three years where the mean June-July maximum temperatures exceeded 20 °C, and which were clearly anomalous from the baseline regime in terms of weather (Suppl. Fig. C1), the positive effect of increasing temperature was lost.

4. Discussion

4.1. Climatic controls of biomass production anomalies

Our analyses of responses of peak biomass to climate variation across 12 years underline the dominant effects of temperature during the peak growth period (June and July) in determining the production of biomass in mountain grasslands. Given the coarseness of the analysis which used biomass estimated via the sward height proxy, climate data from a distant (yet representative) site and land-use type mean data for biomass production, the significance and degree of variance explained of these models is remarkable and supports the robustness and sensitivity of sward height as an indicator for climate response of peak fodder biomass.

Sums of temperature (or growing degree days – GDD) are frequently used for capturing, possibly in combination with radiation or its indicators (modifications by slope and aspect – (Jäger, 2017)), available energy that all physiological processes, and thus growth depend on. Plant phenology is also strongly linked with thresholds in GDD, thereby determining critical periods of vegetative growth and reproduction (Dumont et al., 2015; Duru et al., 2010b; Henebry, 2013). (Jonas et al., 2008) found a positive effect of GDD on biomass production through the snow-free season (considered as the entire growth period) and a more moderate effect of temperature during the month following snow melt across 17 alpine sites in Switzerland, but their analysis did not differentiate months within the growth season. In general, where there were significant relationships between TN or TX and biomass difference there was also a significant relationship with GDD, but it was weaker than respective TN / TX relationships (Suppl. Table 1). Overall, average growth period temperatures were more relevant to TM, TU, UM and across land-use types (Table 1, Fig. 5). But given the strong correlation between temperature variables (Suppl. Mat. C, Fig. C1), the overall thermal energy response may be captured by either. Although GDD may be more integrative, given response thresholds identified with TX (see below) we nevertheless suggest using them in combinations until specific effects and mechanisms are confirmed.

In our analyses snowmelt date (ONSET) was never retained as a significant variable, contrary to (Choler, 2015) at regional level for analyses of growth season NPP. Snowmelt date did actually vary by one month across years (mean snow melt date at site level from the 24th April in 2011 to the 23rd May in 2013) and was only weakly related to peak biomass for higher pastures (SP and UU) (Suppl. Table 1). Yet, snowmelt date was well correlated with mean minimum temperature in May (R^2 = 0.657) and associated number of frosts in May (R^2 = 0.697), which, consistent with expectations (Liu et al., 2018b), decreased peak biomass in less productive vegetation types (TU, UM, SP; Fig. 5). We suspect that the decadal extent of our data set was not enough to clearly detect a direct significant response to snowmelt date that may be captured by longer (e.g. 30 year) time series (Choler, 2015). Additionally, soil rather than air temperature may be a more relevant variable to alpine plant responses to climate (Choler, 2018; Guo et al., 2018), but requires onsite equipment that may not be widely available. Our results nevertheless suggest that simple meteorological variables such as mean temperatures may still be sufficiently informative to account for peak biomass responses.

While drought is considered as a main limiting factor for temperate and mountain grassland production (Calanca et al., 2016; Corona-Lozada et al., 2019; Duru et al., 2010a; Trnka et al., 2006), our analyses did not identify any negative effects of reduced precipitation or soil moisture during the growth period to peak biomass. Soil water recharge from snowmelt may support the first growth cycle regardless of precipitation. We however note that our time series did not include any radically dry springs. The three driest years 2009, 2010, 2012 in our data set did not have reductions in production as compared to prediction by June-July temperatures. The future recurrence of very low snow years (such as 2017) (Verfaillie et al., 2018) may however challenge this buffering capacity. Additionally, drought is likely to affect post-harvest or grazing regrowth (Corona-Lozada et al., 2019; Sautier et al., 2013), especially in the context of extended growing seasons by increasing later summer temperatures (Choler, 2015), but such effects could not be captured with our assessment of climate effects on peak biomass.

Lastly, different land-use types differed in their specific sensitivities to climate parameters. Temperature effects (effect sizes in Table 1) were strongest in TFM, TM and SP, where dominant plants with more exploitative strategies (e.g. lower Leaf Dry Matter Content – LDMC; (Quétier et al., 2007)) may be expected to have more sensitive growth to environmental variation such as temperature and its effects on soil nutrient and moisture availability (Jung et al., 2014; Liancourt et al., 2015; Stampfli et al., 2018). Conversely, the more conservative dominant plants (higher LDMC) with lower phenotypic plasticity found in TU and UU (Grassein et al., 2010) may explain the lower temperature responsiveness of peak biomass in these grasslands (Karlowsky et al., 2018). Also differences across land-use types in climate specific parameter sensitivities mean that different grasslands have asynchronous good and bad years. These differential sensitivities are important for farmers adaptation to climate variability because they imply that different land-use types may be used as resources and adjustments within and across years (Andrieu et al., 2007; Nettier et al., 2017). Specifically, hay from a warm year in mown terraces can buffer e.g. a subsequent poor spring; extreme early summer heat may affect lower grasslands including hay meadows but not summer pastures (if not associated with drought – (Corona-Lozada et al., 2019)); and insensitive grasslands (UU) offer a buffer when a cold season reduces production in other types.

4.2. Anomalies in the three hottest summers on record

Peak biomass production deviated strongly from the temperature-driven relationship for the three hottest summers in our data set (Fig. 4). Other variables, especially early season conditions (May temperatures, frosts) showed responses aligned with other years (Suppl. Fig. 1), but no alternative model incorporating these three years could be found. This suggests the possibility of a regime shift, where baseline driver responses are departed from (Folke et al., 2004). Such departures from the baseline regime would obviously need confirmation across longer time series and more sites. Nevertheless, they may be related to known grassland growth mechanisms.

Firstly there are known heat response thresholds for cool temperate grasslands from 18 °C for grasses to 23 °C for legumes (Duru et al., 2010a), and an overall threshold of 20 °C has been considered for growth modelling (Calanca et al., 2016). (Cremonese et al., 2017) indeed observed severe reduction in photosynthetic activity and growth for *Nardus stricta* grassland during the summer 2015 heat wave in the Italian Alps. Additionally physiological damage from oxidative stress at peak temperatures in the sun, which can excess 40 °C in alpine grasslands (Körner, 1999), has been shown to occur for cool temperate tussock grasses (e.g. *Lolium perenne*, (Soliman et al., 2011)). Secondly, heat accelerates phenological development (Dumont et al., 2015), and may thereby shorten the effective growth period from snow melt, with possible repercussion on maximum vegetative growth. While physiological limitations are likely, we consider this as the most parsimonious explanation for the growth shortage observed during the three hottest years. At our site, we previously observed flowering for the most common grasses to be temperature-driven (e.g. 638 °C.days for dominants *Dactylis glomerata* and *Bromus erectus* in terraced grasslands TFM, TM, TU*;* 494 °C.days for the dominant *Patzkea paniculata* in UM and UU grasslands; Lavorel et al. unpublished). In mountain grasslands, the active vegetative growth period is considered, consistent with these phenological thresholds, to be on average between 300 and 600 °C.days (Nettier, 2016). Its duration has been continuously decreasing over the years in our data set, with 2015 and 2017 being the two shortest (Suppl. Mat. C, Fig. C3).

Further, (De Boeck et al., 2016) found no experimental effect of heat *per se* on growth of alpine vegetation turfs unless it was associated with drought, consistent with other temperate grasslands (Hoover et al., 2014). An analysis across the entire French Alps confirmed that heat waves were associated with reduced annual grassland production only for drought years, and specifically due to lack of summer regrowth (Corona-Lozada et al., 2019). At our site, in 2017 and 2018 growing seasons until July were relatively dry as compared to the average of the study period, while 2015 was rather wet (e.g. July RR, Suppl. Mat. C, Fig. C1A). Nevertheless, the precipitation-related deviation in peak biomass did not align with other years even in fertilised hay meadows (TFM; most sensitive to drought – (Karlowsky et al., 2018)) (negative regression with July RR, Supplementary Fig. 1). We conclude that the three recent extreme years likely each represent unique combinations of direct heat effects, shortened vegetative growth season and drought, but that their recurrence raises concern for a climate tipping point in mountain grassland fodder production. The baseline regime and the anomalies in hottest years need confirmation for longer time series and across a greater geographic extent.

4.3. Implications for fodder production, ecosystem services and farming in mountains

Our analyses showed significant effects of growing season temperatures on mountain fodder production, with differences in driving parameters and sensitivities across land-use types. We also revealed the potential for extreme summer temperature to reduce potential gains from increased average temperatures and decreased spring frosts. Recent observed trends and projections for these climate parameters across the Alps and other European mountains (Beniston et al., 2018; Durand et al., 2009a; Hock et al., 2020; Zubler et al., 2014) thus suggest potential gains in fodder production from increased mean spring temperatures (from + 2 to + 6 °C), which will trade-off with risks from spring frosts and more frequent summer temperature extremes as those observed in the most recent years (Corona-Lozada et al., 2019; Cremonese et al., 2017). Risk from spring frost is of particular concern especially for sensitive high elevation summer pastures given declining length of the snow season, meaning an early start in vegetation growth and potential exposure to damaging frost (Choler, 2015; Klein et al., 2018). Recurrence of extreme summer temperatures induces further uncertainties, with effects yet to be confirmed across the Alps, along with their magnitude. Nevertheless, we emphasized the potential for resilience for farms from their multiple land-uses across the landscape, allowing them to balance shortages from some grasslands with stability or gains from others depending on years. Farmers and herders also use a diversity of management strategies within seasons, years and across years supporting their resilience, whether from adjustment in herd sizes, grazing practices (e.g. adjusting grazing dates and spatial distribution) or from stock management and potential purchase of hay (Nettier et al., 2017). Additionally, because the response of biomass production to climate change underpins those of multiple grassland ecosystem processes and services like soil carbon sequestration, regulation of water quantity and quality or habitat for invertebrates (Lavorel, 2018), observed trends are likely to cascade to multiple impacts for farmers and other land managers in mountains. We conclude that long-term monitoring of mountain grassland biomass production with simple methods and indicators, and analyses of its response to climate parameters is critical for supporting farmers and land managers climate change adaptation (Deléglise et al., 2019).

CRediT authorship contribution statement

Karl Grigulis: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Sandra Lavorel:** Conceptualization, Methodology, Investigation, Resources, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106519.

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