

Main ecological and environmental factors affecting forage yield and quality in alpine summer pastures (NW-Italy, Gran Paradiso National Park)

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Funding information

Gran Paradiso National Park; SUPER-G project (EU Horizon 2020 programme) grant number 774124.

Abstract

Summer pastures in the European Alps play a crucial role in providing high quality forage for grazing livestock and encompass a wide variety of vegetation communities. The main issue of their management is the optimal exploitation of the available forage in relation to environmental constraints, aiming at obtaining the highest forage yield and quality from each vegetation community. In this work, we monitored six different vegetation communities characterized by contrasting topographic features and species compositions throughout the grazing season for two years. We performed botanical and phenological surveys, climate-related measurements, and herbage samplings to assess forage quantity and quality (i.e., digestibility and proximate composition, estimated by near-infrared reflectance spectroscopy). We analysed the influence of climatic, topographic, and vegetation variables on pasture herbage through univariate and multivariate analyses. The cover of wide-leaf grasses primarily promoted biomass production, which was in turn lowered by increasing elevation and slope. On the other hand, a minor effect on forage yield was observed for an increasing cover of sedges and rushes and mean temperatures. Climatic variables (especially water deficit) and advanced phenological stages were the main degrading factors of forage quality in terms of crude protein and digestibility, while enhancing fibre contents. At increasing cover of legumes, fibre content declined and digestibility increased consequently, while the abundance of other non-legume forbs played a significant role in lowering fibre content. Multivariate analysis highlighted the differing influence of single plant species on forage features even within the same functional species pool. However, attention should be paid to the toxicity and low palatability of some plants, especially forbs. Eutrophic vegetation communities, rich in wide-leaf grasses and legumes, could be maintained and enhanced through pastoral management to increase alpine pasture production and quality.

Lombardi Giampiero and Lonati Michele equally contributed to this work.

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KEYWORDS

digestibility, grassland, mountain, phenology, proximate composition, RDA

1 | INTRODUCTION

Alpine summer pastures support the provision of valuable forages for high-quality milk, meat, and other edible products for human nutrition (Gorlier et al., 2012; Ravetto Enri et al., 2017; Renna et al., 2021). Such grasslands play a crucial role in the rural economy of temperate mountains since the forage produced by alpine pastures is generally the sole feed source for grazing livestock during summer (Battaglini et al., 2014; Sturaro et al., 2009). In turn, grazing is the only viable way to manage Alpine pastures, where mechanical agricultural practices are unenforceable. Forage yield and quality change with plant phenology and can be affected by climate, topographic factors, and vegetation composition (Ellenberg, 1988), along with plant phenology (Bätzing, 2003; Bätzing & Bartaletti, 2005; Wingler & Hennessy, 2016). The knowledge of the processes regulating feed provision would represent the baseline to improve livestock management in the alpine farms and establish more efficient plant–animal relations. Indeed, the exploitation of the pasture plant communities should be tuned to gather an optimized forage quality and yield from each of them in terms of both yield and quality.

One of the main factors affecting forage quality through time is the phenological stage as determined by season. Accumulated thermal time (i.e., growing degree days) increase as season advances, directly determining plant phenological development (Ansquer et al., 2009; Schemske et al., 1978). In the initial phase, plant vegetative organs grow both in number and size, leading to high nutritional values of the forage. Then, reproductive organs are generated and fibre fractions increase, while proteins decrease. Finally, at the end of growing season, a progressive loss of carbohydrates and nitrogen compounds occurs, with a consequent drop in forage quality related also to plant senescence (Buxton & Marten, 1989; Sanderson & Wedin, 1989). Additionally, also the interaction between temperature and precipitation is well-known to significantly impact forage productivity and quality (Dumont et al., 2015; Lascano et al., 2001). Temperature affects potential evapotranspiration (Hargreaves & Samani, 1985) which is in turn balanced by precipitation (Wilcox et al., 2003). A marked negative balance between precipitation and evapotranspiration reduces the leaf:stem ratio and thus forage digestibility through an increased proportion of indigestible cell-wall fraction and concurrent reduction in non-structural carbohydrates (Buxton, 1996; Buxton & Marten, 1989; Wilson, 1994). Moreover, the ongoing climate changes emphasize these effects for a number of reasons, such as the increased frequency and intensity of extreme events (Christensen et al., 2007; Pörtner et al., 2019), which are particularly relevant at high elevations for the fragility of ecosystems (Dullinger et al., 2012; Engler et al., 2011; Palombo et al., 2014). Concerning climate change, which has been underway for several decades, a protocol for long-term monitoring of pasture agro-ecosystem quality, called *Alpages Sentinelles*, was implemented in France in the early 2000s (Dobremez et al., 2014).

In the alpine area, the effects of climatic variables on vegetation are emphasized by the harsh environmental conditions due to aspect, elevation, and slope. Aspect determines different light exposition, soil moisture, and nutrient availability, thus representing a direct driver of the botanical composition of pastures (e.g., Yanyan et al., 2017) and an indirect factor affecting biomass productivity and its quality (Dongdong et al., 2020). Increasing elevation determines a decrease in air temperature (0.65°C every 100 m) with consequent effects on vegetation productivity (biomass production is generally lower) and growing season length, which is shorter at higher elevation (Dongdong et al., 2020; Liu et al., 2015). Steep slopes speed up water runoff reducing water availability for plants and enhance evapotranspiration due to more direct and intense solar radiation, so that productivity is often reduced (Liu et al., 2020).

Research on the composition and quality of native grassland forage has been conducted in various ecosystems, from Russian grasslands (e.g. Mikhailova et al., 2000), to those of the Tibetan Plateau (e.g., Liu et al., 2020; Shi et al., 2013) or the Rocky Mountains (e.g., Scasta, 2017), often under controlled conditions (Klein et al., 2007; Xu et al., 2018). In alpine environments, several studies focused on the relations between vegetation composition and forage productivity and quality, highlighting its influence on forage digestibility, palatability, and nutritive value for ruminants (Collomb et al., 2002; Jeangros et al., 1999; Ravetto Enri et al., 2017; Renna et al., 2020; Roukos et al., 2011). Previous studies focused on the differences among botanical families (Daccord et al., 2006; Jeangros et al., 1999), vegetation communities (Andueza et al., 2016), or function groups of species (namely, wide-leaf and narrow-leaf grasses, legumes, forbs, and so forth; for example Duru et al., 2007), while only a few examined the proximate composition of single species (Bovolenta et al., 2008; Marinas et al., 2003). Therefore, a limited number of species have been chemically characterized, whereas alpine grasslands host several hundreds of different species (Landolt et al., 2010). At equal vegetation compositions, the phenological stage has a noteworthy relevance on the forage availability and chemical features (Arzani et al., 2004; Buxton & Marten, 1989; Nelson & Moser, 1994), although evidence on alpine species and communities is still limited (Carrère et al., 2010).

In light of this background, most research concerning the relations between climate, topography, vegetation composition and grassland productivity and quality has been carried out under controlled conditions, in artificial settings, on species-poor temporary grassland or on low-elevation permanent meadows. To our knowledge, no observational studies have been conducted on high-elevation species-rich pastures to explore at a fine scale how such variables directly impact on forage yield, proximate composition, and digestibility. Therefore, we selected six vegetation communities along an elevation and trophic gradient representative of summer pastures of the Western-Italian Alps to assess the relative importance of climatic, topographic,

and vegetational variables in affecting forage production and quality. We hypothesised that increasing temperatures, low precipitations, harsh topographic conditions, and advanced phenological stages would negatively impact forage yield and quality and that the size effect would change in relation to the plant species composition of different vegetation communities. Particularly, we expected that the abundance of specific functional groups would play a primary role in providing valuable forage in terms of both quantity and proximate composition.

2 | MATERIALS AND METHODS

2.1 | Study area

The research was carried out in 2019 and 2020 in the summer pastures of the Lauson valley (Cogne, Aosta Valley Region) within the Gran Paradiso National Park (SAC/SPA IT1201000, North-Western Italy). The area is included in the endalpic xeric district of the Dora Baltea basin, characterized by a continental climate (Braun-Blanquet, 1961; Ozenda, 1985). According to two nearby weather stations (1700 m a.s.l.), mean annual temperature is +4.1°C and mean annual precipitation is about 700 mm (Mercalli & Berro, 2003). The elevation of the valley ranges from 1830 to 3630 m a.s.l. of the peak *Punta Nera della Grivola*. Bedrock is largely composed by gneiss and mica-schists, and to a lesser extent by serpentinite and calc-schists (Carletti, 2015; Le Bayon & Balleve, 2006). Dominant soils are generally shallow, with high gravel content, mainly nutrient-poor and can be identified as Leptosols according to WRB classification. The vegetation consists of semi-natural and natural grasslands rich in species, spread from the lower limit to about 2950 m a.s.l., belonging to several plant communities and varying depending on topographic and edaphic factors. Grasslands dominated by *Festuca violacea* Ser. ex Gaudin are the most widespread at the lower elevations, while *Carex curvula* All. dominates the pastures at the upper parts of the valley. Pastures are regularly exploited by a sheep flock through shepherded grazing between late June and late September.

2.2 | Field surveys

To explore a broad elevation and trophic variability among grasslands, two sites placed at two different elevation belts (Ozenda, 1985) were selected (Figure 1): one at the lower alpine belt (2200–2500 m a.s.l.) and the other one at the upper alpine belt (2500–2800 m a.s.l.). In spring 2019, within each site, three plots were identified along a fertility gradient based on the main vegetation composition, i.e. oligotrophic, mesotrophic, and eutrophic grasslands (Pittarello et al., 2018), as detailed in Table 1. Overall, six different plots corresponding to as many vegetation communities were selected. The three plots at the lower alpine belt were 3.75 × 2.5 m wide, whereas those at the upper alpine belt were 3.75 × 2 m. All the plots were fenced and excluded from grazing. Each plot at the lower and upper belts was subdivided in

five and four 3.75 × 0.5 m parallel strips, respectively, as detailed in Appendix 1. Strips were surveyed only once during summer: from late-June (first strip) to mid-September (fifth strip) at sites in the lower belt and from early-July (first strip) to mid-September (fourth strip) at sites in the upper one. Only four strips (each corresponding to a survey) were surveyed at the upper belt because of the shorter growing season. Within each strip, three vegetation surveys along a 1.25-m linear transects arranged sequentially were carried out. The vegetation survey methodology used was the vertical point-quadrat method (Daget & Poissonet, 1971), according to which the plant species touching a steel needle were identified and recorded at 5-cm intervals (i.e., 25 points of vegetation measurements per transect). The species list was completed by recording all the other vascular plant species within a 50-cm buffer area around the transect.

The number of occurrences of every recorded species was converted to 100 measurements (i.e., it was multiplied by four) to calculate species percentage cover (Pittarello et al., 2019; Ravetto Enri et al., 2020). A cover of 0.3% was attributed to all occasional plant species observed in the buffer area (Tasser & Tappeiner, 2005). Taxonomic nomenclature followed the Checklist of the Italian native vascular flora (Bartolucci et al., 2018).

At each survey date the average plant phenological stage was recorded for each species according to Lambertin scale (Ravetto Enri et al., 2017).

Once plant species composition and phenological stage were surveyed, the sward was cut with a portable lawn-mower (Makita UM104D, Makita Corporation, Anjō, Japan) at 1 cm height on each 1.25 × 0.5 m strip (i.e., three samples per strip and date). The herbage mass was harvested afterwards, immediately stored in polyethylene bags at 4°C in a portable refrigerator, and transported to the laboratory.

Each plot was equipped with temperature data-loggers (Hobo Onset Proseries, 1-h time recording interval) at ground level. An overall value of daily precipitation for the six plots was retrieved from the nearest meteorological station located 2.7 km far from the plots (Valnontey valley, 1700 m a.s.l.).

The same monitoring procedure was used in 2020, reiterating vegetation surveys and herbage sampling at each site within another plot adjoining the one monitored in 2019. Therefore, a total of 162 vegetation surveys were carried out.

2.3 | Forage proximate analyses

Forage samples were oven-dried at 65°C for 48 h and then weighed to compute biomass yields ($t\ ha^{-1}$). The samples were then ground with a Cyclotec mill (Foss Tecator, Hoganäs, Sweden, 1 mm screen) and analysed with near infrared reflectance spectroscopy technique (SpectraStar NIR Analyser–Unity Scientific, Westborough, Massachusetts, USA; INGOT calibration package, Aunir, Towcester, UK) for proximate composition, namely neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL), crude protein (CP), soluble sugars, and dry matter digestibility. Biomass, proximate

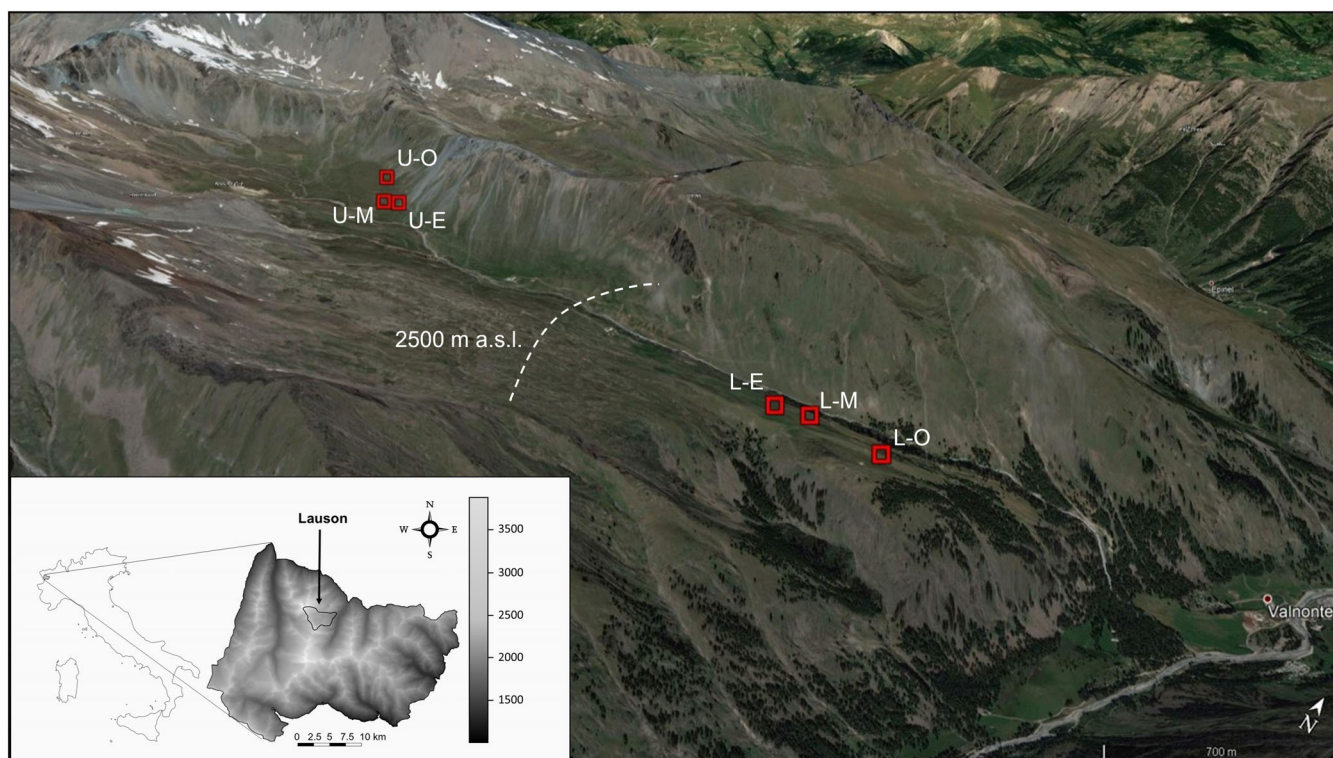


FIGURE 1 Representation of the Lauson valley (Cogne, Gran Paradiso National Park, NW-Italy) including the position of the investigated plots where: L, means lower alpine belt; U, upper alpine belt; O, oligotrophic vegetation; M, mesotrophic vegetation; and E, eutrophic vegetation.

TABLE 1 Description of the identified plots in terms of elevation belt, fertility level, dominant plant species, elevation, and slope.

PLOT	Alpine belt	Vegetation trophic level	Dominant species	Elevation m a.s.l.	Slope °	Southness °
L-O	Lower	Oligotrophic	<i>Festuca violacea</i> and <i>Helianthemum nummularium</i> subsp. <i>grandiflorum</i>	2210	28	31
L-M	Lower	Mesotrophic	<i>Festuca rubra</i> subsp. <i>commutata</i> and <i>Phleum rhaeticum</i>	2280	24	25
L-E	Lower	Eutrophic	<i>F. rubra</i> subsp. <i>commutata</i> and <i>Alchemilla xanthochlora</i> aggr.	2310	0	0
U-O	Upper	Oligotrophic	<i>Carex curvula</i> and <i>Geum montanum</i>	2780	5	140
U-M	Upper	Mesotrophic	<i>Carex sempervirens</i> and <i>Plantago alpina</i>	2730	22	142
U-E	Upper	Eutrophic	<i>P. rhaeticum</i> and <i>Festuca halleri</i> aggr.	2720	5	145

Note: Taxonomic nomenclature follows the Italian vascular checklist (Bartolucci et al., 2018).

composition, and digestibility were considered as response variables in the statistical analyses.

(southness = 180-|aspect-180|) to avoid circular variable issues (Chang et al., 2004).

2.4 | Computation of explanatory variables

2.4.2 | Eco-climatic variables

2.4.1 | Topographic variables

For each plot, aspect, elevation and slope were derived by overlaying the coordinates collected in field (Garmin Etrex30) on a 2 m-resolution digital terrain model (DTM Aosta Valley GeoNavSCT). Spatial analysis was carried out with QGIS 3.16.4 software (QGIS Development team, 2020). The aspect was converted into southness

Hourly temperatures recorded by data loggers were used to calculate the start of the growing season from the first day after snowmelt (Kimball et al., 2014) and the growing degree days. In addition, the mean temperatures between the date of snowmelt and the date of the first survey and, subsequently, between adjacent survey dates, were calculated. Potential evapotranspiration was computed for each plot based on temperatures from the day of snowmelt, according to

Hargreaves equation (Hargreaves & Samani, 1985). Temperatures and precipitations were combined into a synthetic eco-climatic indicator of the water balance for the vegetation (Wilcox et al., 2003), computed as the difference between the total precipitation and the potential evapotranspiration, that is, ΔPrET . Low values of ΔPrET were considered as an indicator of the water stress to which vegetation was subjected.

2.4.3 | Plant community variables

Each recorded plant vascular species was assigned to one of the following functional groups: (i) sedges and rushes; (ii) narrow-leaf grasses (capillary or <1 mm-wide leaves, according to Eggenberg & Möhl, 2013; Pignatti et al., 2017, 2019); (iii) wide-leaf grasses (grasses with leaves wider than 1 mm, according to Eggenberg & Möhl, 2013; Pignatti et al., 2017, 2019); (iv) legumes; (v) other species. We avoided a classification based on single-species identification (e.g., Daget & Poissonet, 1971; Duru et al., 2007) to test the effectiveness of species groups based on an easy-to-measure functional trait that could be used not only by scientific experts, but also by farmers or advisors with a low botanical knowledge. Then, the total percentage cover of each functional group was calculated for every survey.

2.5 | Statistical analyses

To assess the relative importance of topographic, eco-climatic, and plant community variables on forage quantity and quality generalized linear mixed models (GLMM) were performed. The retained explanatory variables were standardized (Z-scores) to assess their relative importance in the models (β coefficients). Biomass, being a positive and continuous variable, was modelled with a Gamma (Log link) instead of a Gaussian distribution family as it showed a lower Akaike's Information Criterion (Zuur et al., 2009). Proximate composition and digestibility, being percentage data, were rescaled to 0 and 1 to be modelled with a Beta distribution. The transformation $[\ln(n-1) + 0.5]/n$ (n = sample size) was applied to avoid 0 and 1 values (Smithson & Verkuilen, 2006), which are not allowed by the Beta distribution family. The dates of survey nested within the six plots were considered as random factor to account for spatio-temporal autocorrelation. Significance was set at $p < .05$. GLMM was performed using R software, version 4.03 (R Core Team, 2020), with the "glmmTMB" function of "glmmTMB" package (Magnusson et al., 2017).

A multivariate constrained ordination was performed to highlight the relations between vegetation composition and forage quantity and quality. The forage biomass and chemical matrix was used as response matrix, constrained by the frequencies of occurrence of each species. A supplementary matrix composed by the eco-climatic, topographic, and plant community variables was supplied afterwards. Being the axis length of a preliminary Detrended Correspondence Analysis (DCA) shorter than four, a Redundancy Analysis (RDA) was performed (Ter Braak & Smilauer, 2002). DCA and RDA were carried

out with CANOCO 4.5 (Ithaca, NY, USA). A Monte Carlo permutation test with 999 permutations was used to assess the significance of the RDA.

3 | RESULTS

3.1 | Climate and plant communities

The growing season started about 10 days earlier in 2020 compared to 2019 (15 May 2019 vs 5 May 2020). Mean temperature was lower during 2019 than during 2020 while total rainfall during the two growing seasons was similar, but it was more evenly distributed in 2019 than in 2020. In 2019, ΔPrET was characterized by a smoother decline throughout the season compared to 2020, with several brief increments according to rain events, almost absent in 2020 (Figure 2).

A total of 133 different vascular species was recorded in the six plots (see Appendix 3 for the complete list of species). Among these, six were sedges and rushes, eight narrow-leaf grasses, 12 wide-leaf grasses, 10 legumes, and 93 other species. Wide-leaf grasses and other species were the dominant functional species pools in terms of species cover (Figure 3). Sedges and rushes were less represented in the studied grasslands, reaching maximum cover of about 35% in the U-M plot dominated by *Carex sempervirens* Vill., while legumes, even if recorded in every survey plot with at least 4% of average cover, did not overcome the 25% average cover.

3.2 | Forage yield and quality

The forage yield and quality of the six vegetation communities in terms of biomass, proximate composition and digestibility are reported in Table 2. Average biomass ranged between 0.1 and 3.3 t ha⁻¹, with lowest yields at the higher elevation in the oligotrophic plot (U-O) and highest values at the lower elevation in the eutrophic plot (L-E). Plot L-E was characterized by a biomass two to three folds higher compared to other sites.

The fibre fraction (NDF, ADF, ADL) increased throughout the season in all the sites and higher values were found in plot U-M. NDF and ADF lowest average values were measured at plot U-O (365.8 and 174.2 g kg⁻¹, respectively), while for ADL at plot U-E (25.5 g kg⁻¹). Average mean CP was highest at the lower elevation in the eutrophic plot with content up to 178.9 g kg⁻¹, decreasing over time at all sites from T1 to T5. The lowest content of CP was recorded at plots U-M and U-O at the end of the growing season (less than 60 g kg⁻¹). Soluble sugars decreased during the season, except at plot U-E where contents were always higher than in all the other sites.

For all the plots, digestibility decreased over time. Both eutrophic plots were characterized by a high digestibility (around 75% at T1) while the lowest mean values were found in plots L-O and U-M at T5 (around 45%).

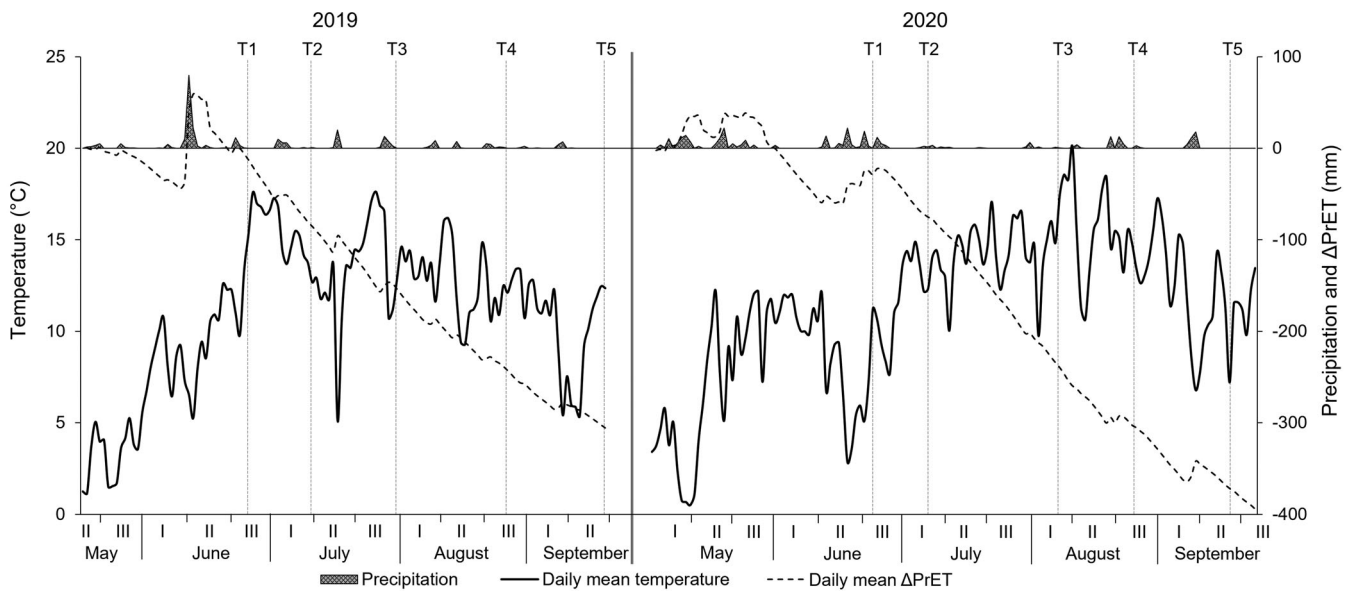


FIGURE 2 Distribution of daily mean temperature in °C, daily precipitation in mm and Δ PrET (water balance between precipitation and evapotranspiration) in mm across the growing seasons 2019 (left) and 2020 (right) from the day of snow melt in the Lauson valley. Months are subdivided into decades (I to III) and T1 to T5 represent the survey dates in 2019 and 2020.

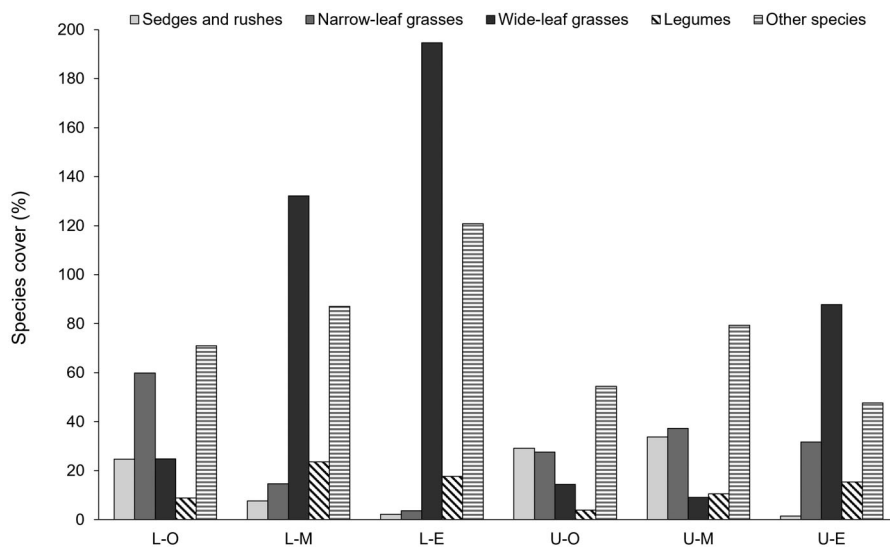


FIGURE 3 Cover (%) of the forage functional groups of species in the six plots where: L, means lower elevation belt; U, upper elevation belt; O, oligotrophic vegetation; M, mesotrophic vegetation; and E, eutrophic vegetation.

3.3 | Effects of climatic, topographic, and plant community variables on forage features

Among explanatory variables, southness, days from snow melt, and GDD were highly collinear with elevation, Δ prET, and phenology (Pearson $r > |0.70|$) and, thus, excluded from further analyses (Appendix 2). All other variables were not correlated each other and they were included in the GLMM model (Table 3).

Elevation was the main factor in conditioning grassland biomass: as it increased, forage production decreased. A high wide-leaf grass cover resulted in a higher biomass while slope, instead, reduced forage yield. Increasing cover of sedges and rushes and mean temperatures enhanced biomass production but with a lower relative importance

compared to other significant variables. Δ PrET contribution was weak, while plant phenology, cover of narrow-leaf grasses, legumes, and other species had no significant role in biomass production.

Decreasing Δ PrET (i.e., toward drought conditions) and later phenological stages led to higher fibre content (NDF, ADF, ADL) with greater relative importance than other significant variables. Higher elevation was weakly significant in lowering NDF content, while the cover of other species and legumes were significant but of relatively lower importance. Among plant community variables, only the cover of the other species influenced significantly ADF content with a slight lowering effect. The increase in slope and cover of sedges and rushes were weakly significant in enhancing ADL content while increasing cover of wide-leaf grasses and narrow-leaf grasses lowered it in turn.

TABLE 2 Average (summers 2019–2020) mean and standard error (s.e.) values of forage productivity and proximate composition of the investigated vegetation plots of the Lauson valley along the growing season (from T1 to T5 dates of survey).

PLOT		Biomass (t ha ⁻¹)		Crude protein (g kg ⁻¹)		NDF (g kg ⁻¹)		ADF (g kg ⁻¹)		ADL (g kg ⁻¹)		Soluble sugars (g kg ⁻¹)		Digestibility (%)	
		mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
L-O	T1	0.5	0.10	133.1	8.02	417.1	37.07	202.5	20.30	36.1	3.88	114.4	21.57	67.0	1.32
	T2	0.5	0.06	118.8	5.18	434.2	13.96	212.6	6.56	39.4	2.64	108.5	13.66	64.9	0.92
	T3	0.4	0.09	97.7	5.27	476.6	19.73	240.2	9.66	45.7	2.30	99.3	9.49	59.7	1.38
	T4	0.5	0.10	90.0	3.69	534.3	32.79	279.4	19.49	54.8	1.77	66.4	6.59	53.9	2.62
	T5	0.4	0.05	68.5	5.57	615.7	33.15	329.8	15.61	64.9	2.05	41.9	6.03	47.6	1.66
L-M	T1	0.8	0.17	159.7	15.01	440.5	17.15	194.7	7.71	27.1	0.78	129.4	22.62	72.2	0.73
	T2	1.0	0.13	134.7	8.41	431.8	8.93	200.3	3.77	29.5	0.87	134.8	10.12	72.1	0.86
	T3	0.7	0.09	98.5	3.39	456.7	17.35	234.1	8.53	43.4	1.07	108.8	5.06	64.0	0.86
	T4	1.1	0.21	88.8	3.45	526.3	15.30	274.3	6.64	52.9	1.26	79.1	7.25	58.7	1.30
	T5	0.8	0.14	66.3	5.25	605.9	8.20	323.4	4.14	63.6	1.38	45.7	4.48	51.7	0.55
L-E	T1	1.8	0.49	178.9	25.23	438.9	14.29	199.1	6.78	27.5	1.42	98.2	23.15	73.3	0.95
	T2	3.3	0.55	149.0	12.99	459.4	10.57	214.0	5.74	30.1	0.66	110.4	17.44	71.9	0.63
	T3	3.0	0.34	125.0	16.59	480.4	10.05	232.8	6.69	36.3	1.51	100.6	12.04	68.6	1.65
	T4	2.8	0.34	108.6	14.18	527.5	23.88	263.0	14.91	43.5	3.44	77.5	6.39	63.7	3.04
	T5	2.3	0.20	92.2	4.82	564.2	23.53	286.4	12.27	51.8	2.80	59.0	6.02	60.6	2.01
U-O	T2	0.2	0.03	142.7	9.69	365.8	12.38	174.2	4.83	28.2	0.51	117.6	7.17	70.1	0.98
	T3	0.2	0.03	99.3	15.66	431.1	36.55	217.6	18.26	39.3	3.92	100.2	10.65	63.8	1.14
	T4	0.3	0.09	84.8	8.10	468.5	42.67	244.2	23.37	46.7	3.30	89.0	4.59	58.6	1.47
	T5	0.1	0.02	56.3	3.07	570.8	23.71	300.0	14.59	58.9	4.19	52.3	12.21	52.4	2.66
U-M	T2	0.2	0.04	115.8	3.13	471.4	16.58	237.6	12.37	46.8	4.16	98.1	8.76	65.6	2.88
	T3	0.4	0.11	96.0	4.73	496.3	23.83	264.9	19.59	56.3	5.29	87.2	12.01	60.3	2.99
	T4	0.5	0.19	76.8	3.59	523.6	19.39	283.6	10.62	62.8	2.82	74.7	7.93	56.5	2.03
	T5	0.3	0.05	58.1	3.20	624.1	14.38	346.2	12.03	74.5	4.06	37.1	8.00	47.3	2.44
U-E	T2	0.4	0.05	130.6	8.83	421.2	13.08	177.9	5.06	25.5	1.36	148.4	14.81	76.4	0.71
	T3	0.4	0.09	92.8	4.37	462.3	13.73	218.7	2.84	41.9	3.54	134.7	8.80	67.4	1.09
	T4	0.6	0.12	87.8	5.93	475.0	10.90	218.3	4.27	44.3	1.88	146.4	8.81	67.9	0.61
	T5	0.3	0.08	72.5	5.56	566.8	22.72	265.7	16.00	50.8	3.52	138.1	17.80	62.4	2.20

Note: L, means lower alpine belt; U, upper alpine belt; O, oligotrophic vegetation; M, mesotrophic vegetation; and E, eutrophic vegetation. NDF, neutral detergent fibre; ADF, acid detergent fibre; ADL, acid detergent lignin.

Elevation and cover of wide-leaf grasses showed positive effects on soluble sugars, while weaker relationships were observed with plant phenology and Δ PrET. Decreasing Δ PrET and later phenological stages negatively affected crude protein with a ten-fold higher relative importance compared to other significant variables, i.e., slope, elevation, wide-leaf grasses, and temperature, all showing a negative influence on crude protein content. The factors affecting digestibility were, in order of importance, Δ PrET (positively), phenology (negatively), elevation (negatively but weakly significant), the cover of sedges and rushes (negatively), and the cover of legumes (positively).

The RDA was statistically significant ($p < .001$, $R^2_{adj} = 0.56$) and 78.2% and 7.6% of the total variance were explained by the first and second axes, respectively (Figure 4). The plant species separated along

the first axis mainly according to their digestibility, which also confirmed its relations with Δ PrET and legume cover. Crude protein and soluble sugar content (on the left side of the graph) opposed to fibre content (NDF, ADF, ADL) and to phenology, temperature, and sedges and rushes cover (on the right). Biomass, instead, was less clearly associated to specific factors or plants, being approximately centred in the middle. Plant species associated to high digestibility and protein content belonged mainly to the functional groups of the other species (e.g., *Ranunculus kuepferi* Greuter & Burdet, *Ranunculus villarsii* DC., *Geum montanum* L.), wide-leaf grasses (e.g., *Poa alpina* L., *Phleum rhaeticum* (Humphries) Rauschert, *Trisetaria flavescens* (L.) Baumg.), and legumes (e.g., *Lotus corniculatus* subsp. *alpinus* (DC.) Rothm., *Trifolium pallescens* Schreb.). Conversely, species belonging to narrow-leaf grasses (e.g., *Festuca violacea*, *Nardus stricta* L.) and sedges (e.g. *Carex*

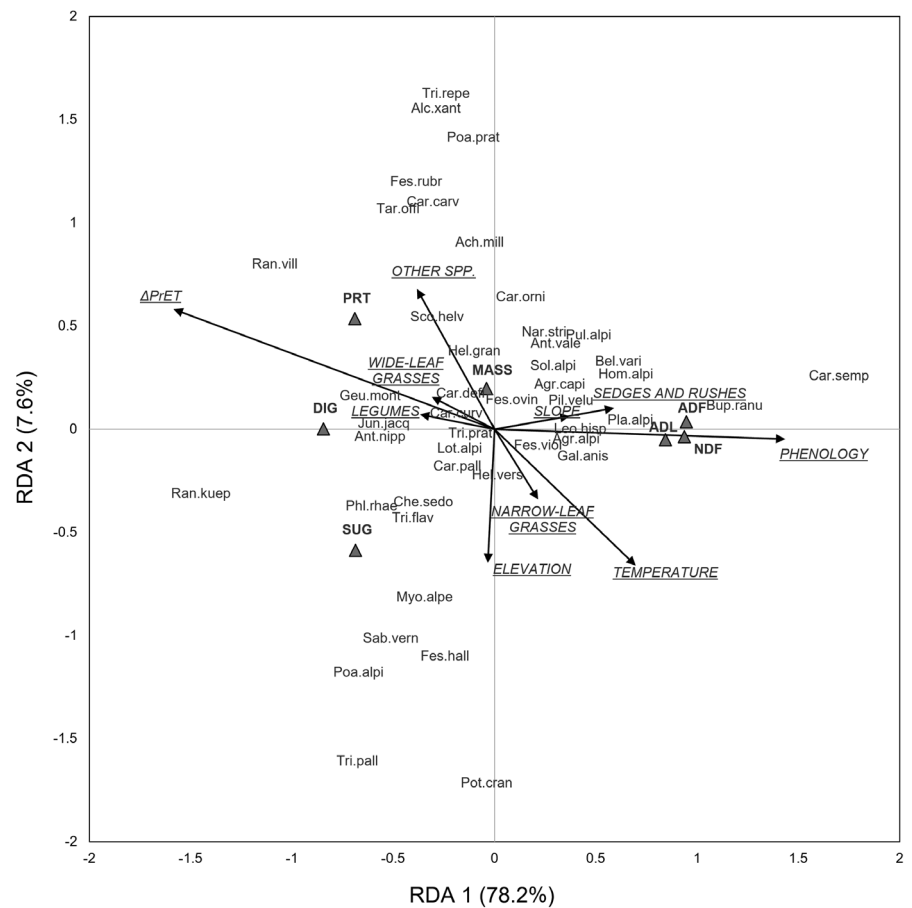
TABLE 3 Results of Generalized Linear Mixed Model (GLMM) showing the effects of eco-climatic (mean temperature and Δ PrET) and topographic factors, plant community functional groups of species, and phenological stage on forage productivity (biomass), proximate composition (NDF, ADF, ADL, soluble sugar, and crude protein), and digestibility.

Variables	Unit	Biomass ¹			NDF ²			ADF ²			ADL ²			Soluble sugar ²			Crude protein ²			Digestibility ²		
		Rank	β	Sig.	Rank	β	Sig.	Rank	β	Sig.	Rank	β	Sig.	Rank	β	Sig.	Rank	β	Sig.	Rank	β	Sig.
Intercept			-0.54	***		-0.03	n.s.		-1.14	***		-0.2	**		-2.3	***		-2.19	***		0.54	***
Eco-climatic																						
Mean temperature	°C	5	0.15	**		0	n.s.		-0.01	n.s.		-0.03	n.s.		0.03	n.s.	6	-0.06	**		-0.02	n.s.
Δ PrET	/	6	0.09	†	1	-0.18	***	1	-0.15	***	1	-0.29	***	4	0.1	*	1	0.2	***	1	0.18	***
Topographic																						
Slope	°deg	3	-0.38	*		0	n.s.		0.02	n.s.	3	0.16	†		0.08	n.s.	3	-0.08	**		0.07	n.s.
Elevation	m	1	-0.58	***	2	-0.11	†		-0.09	n.s.		-0.02	n.s.	1	0.24	*	4	-0.08	**	3	-0.07	†
Plant community cover %																						
Sedges and rushes		4	0.18	***		0.03	n.s.		0.02	n.s.	5	0.05	†		-0.03	n.s.		-0.03	n.s.	4	-0.04	**
Narrow-leaf grasses			0.06	n.s.		0.00	n.s.		0.00	n.s.	6	-0.05	†		0.03	n.s.		-0.01	n.s.		0.00	n.s.
Wide-leaf grasses		2	0.42	***		0.03	n.s.		-0.02	n.s.	4	-0.12	*	2	0.23	***	5	-0.08	*		0.03	n.s.
Legumes			0.05	n.s.	5	-0.03	*		-0.01	n.s.		0.01	n.s.		-0.01	n.s.		0.02	n.s.	5	0.03	*
Other species			-0.02	n.s.	4	-0.06	***	3	-0.03	*		0.01	n.s.		0.03	n.s.		-0.01	n.s.		0.01	n.s.
Phenology	stage		-0.01	n.s.	3	0.08	***	2	0.09	***	2	0.18	***	3	-0.18	***	2	-0.1	***	2	-0.11	***

Note: Asterisks and cross-shaped symbol represent statistical significance: ***, $p < .001$; **, $p < .01$; *, $p < .05$; †, <0.1 weak significant; n.s., not significant ($p \geq .05$).

Abbreviations: ADF, acid detergent fibre; ADL, acid detergent lignin; NDF, neutral detergent fibre; Δ PrET, water balance between precipitation and evapotranspiration. ¹Family: Gamma, ²Family: Beta.

FIGURE 4 RDA ordination bi-plot showing the relations between forage yield and quality variables (triangles) and plant species composition (species are identified by codes; full names are provided in Appendix 3). Eco-climatic variables, phenology, topography, and forage functional groups are projected as passive variables (arrows). MASS, forage yield; DIG, dry matter digestibility; PRT, crude protein; SUG, soluble sugars; NDF, neutral detergent fibre; ADF, acid detergent fibre; ADL, acid detergent lignin; Δ PrET, water balance between precipitation and evapotranspiration.



sempervirens) were linked to a higher fibre content. The species were distributed on the second axis along an elevation gradient, with high-elevation species such as *Potentilla crantzii* (Crantz) Beck ex Fritsch and *Festuca halleri* aggr. at the bottom and *Taraxacum officinale* aggr., *Achillea millefolium* aggr., and *Festuca rubra* L. subsp. *commutata* (Gaudin) Markgr.-Dann. in the upper part. Among the proximate compounds, only sugar and protein content were clearly separated on the second axis, confirming their significant relationship with the elevation highlighted by the univariate analysis.

4 | DISCUSSION

Our research provided novel information concerning the relative importance of eco-climatic, topographic, and plant community variables in affecting forage yield and quality in alpine pastures. Several other studies have been carried out with this aim in controlled conditions on mono-specific or species-poor temporary grasslands or in low elevation meadows, mainly varying single factors and achieving contrasting outcomes (Bai et al., 2013; Cantarel et al., 2013; Dumont et al., 2015; Peratoner et al., 2020; Sanaullah et al., 2014). Our study should be regarded as one of the first ones carried out in a natural setting on species-rich alpine permanent pastures.

The effect of eco-climatic variables plays a leading role in determining the grassland productivity and forage quality, as the robust

information provided by the statistical analyses highlighted. Particularly, increasing Δ PrET determined a strong increase of fibre contents and a reduction of crude protein and therefore digestibility. Water deficit in the short alpine growing season enhances the senescence of leaves (Buxton, 1996); as a consequence, crude protein, and soluble sugars are relocated from leaves to roots and the forage nutritive value declines (Durand et al., 2010).

Overall, topographic and plant community variables had a significant but subordinate influence compared to water balance, temperature, and the phenological stage of the species. Specifically, water balance was particularly relevant, even if with differing magnitudes when compared to the effects exerted by the cover of functional species pools. Indeed, for fibre contents, the cover of functional pools had no more than half of the relative importance of Δ PrET as for wide-leaf grass cover on ADL, while such ratio did not exceed one sixth in the case of legume cover on NDF. Grass cover decreased with elevation being grasses replaced by other species, which is common in alpine pastures (Körner, 2003). However, their role in relation to productivity was of major importance, as expected. In particular, the cover of wide-leaf grasses was the most important factor positively affecting forage yield, as already found for grasslands at lower elevation (Duru et al., 2007), with a relative importance lower only than elevation, confirming our initial hypothesis. Surprisingly, the cover of sedges and rushes (e.g., *Carex sempervirens* Vill. or *Carex curvula* All.), which dominate many high-elevation pastures in the Alps (Cavallero

et al., 2007), was important in enhancing biomass production as well. Interestingly, our models delineated a not negligible effect of the cover of the other species in lowering fibre content (NDF and ADF), even if this pool consisted of a large spectrum of species having likely contrasting effects (Carrère et al., 2010). The general low fibre content of the other species could be likely related to the high leaf:stem ratio (stems are often reduced to a few millimetres) and to the bigger reproductive structures in comparison with other plant organs (Fabbro & Körner, 2004; Körner et al., 1989). The contribution of alpine non-legume forbs is generally underestimated in explaining forage quality, likely because of the high variability of the species growing in alpine grasslands. Therefore, the knowledge about their role still has to be addressed by future research. For instance, species belonging to the Plantaginaceae family seem to negatively impact forage quality, while species belonging to Rosaceae and Ranunculaceae families enhance forage chemical quality (Jeangros et al., 1999). As we supposed, legumes played a significant role in determining digestibility, despite their low cover in our study area, as observed in most of legume species in lowland grasslands (Dewhurst et al., 2009; Vasiljević et al., 2009). On the other hand, our model showed a negative effect of sedges and rushes on digestibility despite they have been recognized as fairly good digestible feed (Jeangros et al., 1999). The position of some species in the multivariate space confirmed our outcome, showing for instance *Carex sempervirens* at the opposite to digestibility. Notably, the cover of grasses (both narrow- and wide-leaf) did not significantly affect forage digestibility even if wide-leaf grasses had a major role in explaining soluble sugars content, which are the primary source of the readily available energy for rumen fermentations. Therefore, the increase of eutrophic vegetation communities with relevant cover of wide-leaf grasses through pastoral management should be regarded as a target to obtain valuable forages with high yield and sugar concentrations and low lignin content (Perotti et al., 2018). The methodology applied in the present trial was based on a two-levels classification of grass species (i.e., narrow-leaf and broad-leaf), but other research groups successfully implemented different classifications, based on other functional or chemical traits. For instance, Ansquer et al. (2004), Duru et al. (2008), and Cruz et al. (2010) discriminate 39 different grass species in four or six groups according to their dry matter content and proved that such functional types can characterize herbage growth patterns. Unfortunately, it was not possible to apply the same classifications to our case study since a number of species found during our trial including also some grasses dominating or highly abundant in our study sites, such as *Bellardiocloa variegata* (Lam.) Kerguelén, *Festuca halleri* aggr., *Festuca violacea*, and *Poa alpina*, were not listed by those studies. Thus, it would be worth to extend such dry-matter-based classifications to those grass species not yet considered in the cited literature but widespread in Alpine pastures.

Further, our study encompassing the entire growing season with several surveying dates pointed out the relevant effect of plant senescence due to phenological advancement on forage quality, in accordance to our expectation. As the plants mature, the leaf:stem ratio decreases and the cell wall thickens; lignin content increases and physically opposes microbial enzymes acting as a barrier to digestibility

(Demarquilly & Jarrige, 1981; Moore & Jung, 2001). This was confirmed by our study, as phenology impacted fibre contents, crude protein, and digestibility with a magnitude second only to Δ PrET, highlighting the importance of the choice of the grazing period for maximizing the exploitation of forage resources. Similar findings were gathered by Carrère et al. (2010) on lowland grasslands.

Multivariate relationships between proximate composition and single species cover highlighted the differing effect of botanical composition on forage quality. The position of temperature, Δ PrET, and phenology in the ordination plot was consistent with the main outcomes of the GLMM displaying similar relationships with forage chemical composition. Likewise, looking at the position of the species functional groups, narrow-leaf grasses and sedges and rushes were positioned toward the chemical parameters related to fibre (NDF, ADF, ADL), while legumes, wide-leaf grasses, and other species were closer to crude protein, soluble sugar, and digestibility. Nevertheless, the single-species position in the plot revealed a few exceptions. For instance, the wide-leaf grass *Agrostis capillaris* L. was positioned close to fibre fractions, far from most of the other wide-leaf grasses. Among the other functional groups further exceptions could be observed when compared to the overall relations between the functional species pool and the forage features. For instance, *Juncus jacquini* L. was closer to digestibility and farther from fibre than the other species belonging to sedges and rushes pool, while *Buplerum ranunculoides* L. showed an opposite pattern compared to the other species functional pool. Despite the close connection of the other species functional pool with digestibility, it has to be kept in mind that some forbs are toxic for livestock (e.g., *Ranunculus* spp., Burriel, 1992; Majak, 2001) or very little consumed (e.g., *Cardus* spp., *Gentiana* spp.). The same applies to some graminoids, such as *Anthoxanthum odoratum* aggr. or *Trisetaria flavescens*, both having small amounts of toxic compounds (Majak, 2001; Runciman et al., 2002). However, the presence of toxic and unpalatable compounds and organs in pasture plants has been poorly studied by the international scientific community and incomplete or ambiguous information can be found (e.g., Therrien et al., 1962). Moreover, the effect of such species on grazer metabolism can change considerably due to plant phenological stage, plant organ (i.e., leaf, stem, inflorescence, etc.), and herbivore species or category (e.g., Iussig et al., 2015). The role of legume functional pool was less clear, as such species were remarkably dispersed in the multivariate bi-plot due to their heterogeneous proximate composition. This may explain the negligible influence, partially unexpected, of legumes cover on protein content assessed by univariate analyses. Such ambiguous evidence within the legume functional group highlighted the lack of knowledge about its forage quality in the alpine belt. Further research, not only on legumes but on all other functional pools as well, is needed to assess the relationships between individual species and the chemical quality of alpine forages, as few investigations on a limited number of species has so far been carried out (Bovolenta et al., 2008; Marinas et al., 2003). According to such outcomes, we suggest that increasing the cover of eutrophic vegetation communities hosting abundant wide-leaf grasses, legumes, and other species, coupled with a decrease of oligotrophic communities (i.e., with high

cover of narrow-leaf grasses or sedges and rushes) would favour forage yield and quality of alpine summer pastures, tempering the negative effect of adverse climatic factors.

5 | CONCLUSION

Despite the more complex interactions between factors that occur in natural settings compared to controlled experiments, our research provided clear information about the primary role of eco-climatic variables in affecting forage yield and quality of summer pastures. Particularly, water balance and plant phenology strongly impacted forage productivity and proximate composition. According to these outcomes, in the future scenarios of climate change alpine pastures will face the dramatic effects of the increasing frequency of heatwaves and droughts. Our study also provided additional information about the effects of vegetation composition of alpine grassland ecosystems characterized by high species diversity on forage features, depending on species composition. However, we also found that the abundance of wide-leaf grasses and legumes were particularly relevant in enhancing forage yield and quality, confirming our initial hypothesis.

Our study was based on a limited (rather representative) sample of Alpine pastures, so that, to gather more general knowledge on this research topic, similar trials should be carried out also in other mountain environments, exploring contrasting situations in terms of vegetation communities (e.g., in nutrient-rich pastures), topographic attributes (e.g., in north-facing aspects), and eco-climatic features (e.g., in wetter conditions). Additional variables which can affect forage productivity and quality should also be considered, such as soil chemical properties, drying effect of wind, or actual insolation of grassland vegetation. Similarly, the evaluation of forage production could be studied along with other ecosystem services, such as biodiversity, pollination, water regulation, and soil erosion control.

AUTHOR CONTRIBUTIONS

Andrea Mainetti: conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (lead); Methodology (supporting); Writing-original draft (lead); Supervision (supporting); Project administration (supporting); Funding acquisition (supporting). Simone Ravetto Enri: conceptualization (supporting); Data curation (lead); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing-original draft (supporting); Supervision (supporting); Project administration (supporting). Marco Pittarello: Data curation (supporting); Formal analysis (lead); Methodology (supporting); Writing-original draft (supporting). Giampiero Lombardi: Methodology (supporting); Writing-original draft (supporting); Supervision (supporting); Project administration (lead); Funding acquisition (lead). Michele Lonati: conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Methodology (lead); Writing-original draft (supporting); Supervision (lead); Project administration (supporting); Funding acquisition (supporting).

ACKNOWLEDGEMENTS

The authors thank the Gran Paradiso National Park for technical assistance and particularly Laura Poggio for her role in promoting this research. We are grateful to Davide Barberis, Ginevra Nota, Rebecca Pagani, and Laurent Perron for their work in the field and in the laboratory.

FUNDING INFORMATION

The project was funded by Gran Paradiso National Park and by SUPER-G project (EU Horizon 2020 programme) grant number 774124.

CONFLICT OF INTEREST STATEMENT

Authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the corresponding author on reasonable request.

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SUPPORTING INFORMATION

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How to cite this article: Mainetti, A., Ravetto Enri, S., Pittarello, M., Lombardi, G., & Lonati, M. (2023). Main ecological and environmental factors affecting forage yield and quality in alpine summer pastures (NW-Italy, Gran Paradiso National Park). *Grass and Forage Science*, 1–14. <https://doi.org/10.1111/gfs.12609>