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CICLO: XXXIV

PLANT DIVERSITY, SOIL PROPERTIES AND
AGRONOMIC FEATURES OF ALPINE VEGETATION
COMMUNITIES ALONG ECOLOGICAL GRADIENTS
IN THE NW-ITALY

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1. Preface

Ecosystem Services of alpine vegetation communities

The multiple benefits offered by nature to human society are defined as Ecosystem Services (hereafter ES) (Butler and Oluoch-Kosura, 2006; Seppelt et al., 2011; Diaz et al., 2018). Natural ecosystems support life among others by purifying air and fresh water, by regulating climate and soil fertility, by recycling nutrients and waste, by perpetuating biological diversity and providing a wealth of resources. Many studies by a variety of authors and in particular by the Millennium Ecosystem Assessment have classed ES in four macro-categories, namely regulating, provisioning, supporting, and cultural ES (De Groot et al., 2002; MA, 2005; Carpenter et al., 2006; Boyd and Banzhaf, 2007; Jordan et al., 2010). Biotic and abiotic environmental and anthropogenic factors and their interaction shape and control the supply of ES which exhibit complex relationships (Braat and de Groot, 2012, Yang et al., 2020a, Yang et al., 2020b; Alemu et al., 2021).

Overall, natural and semi-natural terrestrial ecosystems have a great capacity to provide ES, as they generally generate complex ecosystems in terms of biological communities and relationships with the environment (Bauhus et al., 2010; Decocq et al., 2016). They therefore provide a surplus supply of ES that are typically exploited by urban settings, areas which offer far fewer ES than they require (Burkhard et al., 2009; 2014). In these terms, mountain environments, typically sparsely urbanised and rich in natural and semi-natural ecosystems play a fundamental role in supporting human activities (Lavorel et al., 2011; Briner et al., 2012).

In the Alps, mountain ecosystems harbour an extraordinary diversity of habitats and plants, especially in the Alpine belt where only highly specialised entities of outstanding naturalistic interest are allowed to survive. All ES, be they provisioning or regulating or others, are intimately related to plant diversity (Pereira et al., 2005; Gamfeldt et al., 2008). Even though extensively managed mountain areas are often perceived as economically not-profitable regions (Grêt-Regamey et al., 2008), they can be considered an underestimated environmental asset of Europe (Hazeu et al., 2010; Huber et al., 2013). Alpine ecosystems provide to the society a broad list of services and goods, as protection against natural hazards (e.g., floods, avalanches, and landslides), carbon sequestration and storage in soil and biomass, or renewable natural resources such as timber and fodder for livestock (EEA, 2010). Among them, fresh forage represents one of the main products offered

by the ecosystems developing in the alpine belt, which in summer is generally the only feed for grazing livestock (Sturaro et al., 2009). It serves as the basis for high-quality healthy food as dairy products (Renna et al., 2020), whose demand is constantly growing (Grunert, 2013).

The present thesis aims to explore the delivery of ES (related to plant diversity, soil properties and agronomic features) provided by vegetation communities located along different ecological gradients in the Alpine environment.

Ecological gradients along proglacial primary successions

In the Alps, mountain environments are often marked by harsh topography and extreme conditions for life. The processes that lead to the stabilisation of slopes and debris through plant colonisation are crucial for the persistence of man in mountain areas and in adjacent lowland regions. Since the end of the Little Ice Age (ca. 1850), large areas of rock and debris have been exposed to weathering, as glaciers receded due to ongoing anthropogenic climate change (Dyurgerov and Meier, 2000; Zemp et al., 2006; Paul et al., 2004; Eichel, 2019). This rapid retreat of the glaciers is causing a high rate of sediment release (Koppes and Hallet, 2002) which, together with the increased frequency of intense water precipitation events, even at high altitudes, poses a risk in terms of floods, debris flows and landslides (Pörtner et al., 2019). Plant colonisation of these so-called proglacial areas stabilises and anchors the silty inorganic material, prevents soil erosion and flooding and enhances soil fertility and nutrient cycling, thus providing multiple benefits to human society. Therefore, exploring the dynamics along the ecological gradients that lead to the establishment and development of alpine vegetation communities is relevant to understand the mechanisms that regulate the triggering of ES delivery.

Proglacial primary successions have been often studied along time gradients in the form of space for time substitution, i.e. chronosequences (Pickett, 1989). This approach is feasible when the history and geography of glacial advances and retreats is known, especially when they have not been associated with intense disturbance phenomena such as huge rock falls, collapses or debris flows. More rarely they have been studied by revisiting permanent plots (Fickert and Grüninger, 2018). The first studies on chronosequences date back to the end of the 19th and the beginning of the 20th century (Coaz, 1887; Von

Klebensberg, 1913; Lüdi, 1921; 1934; Oechslin, 1935). This was followed by a great deal of research worldwide and in the Alps, exploring differences along gradients of soil formation (e.g. Burga, 1999; Burga et al., 2010; Egli et al., 2010; D'Amico et al., 2014), plant colonisation (e.g. Andreis et al., 2001; Caccianiga and Andreis, 2004; Raffl et al., 2006; Cannone et al., 2008) and on other biotic and abiotic components (e.g. Matthews, 1992; Bernasconi et al., 2011; Jumpponen et al., 2012; Ciccazzo et al., 2016). These studies stated that over time, mineral weathering, atmospheric deposition and microbial communities affect the C:N:P stoichiometry of the soil-microorganisms-plant system. The availability of soil nutrients and the disturbance regime influence the patterns of pioneer, early-, mid- to late-successional species replacement. Along with the consolidation of the debris, the accumulation of organic carbon (hereafter C) takes place in the soil, contributing to the regulation of C balance. Topsoil organic C accumulation rate is high in the first phases of plant colonisation and the amounts stored in soil reach not-negligible levels after about one century, albeit with a high variability of the stability of C forms and between the different studied sites (Burga et al., 2010; Egli et al., 2012; Eckmeier et al., 2013; Khedim et al., 2020). However, in the proglacial areas left free by ice since the end of Little Ice Age (ca. 1300-1850), time was not sufficient for the establishment of stable alpine grassland communities (Andreis et al., 2001), which are responsible for greater accumulation of soil organic C (Bullock et al., 2011).

The first specific objective of the present thesis is the evaluation of pioneer and late-successional plant species patterns along a high-altitude proglacial chronosequence in the Western Italian Alps (Lauson glacier, Gran Paradiso National Park). We focused especially on the role of vegetation succession, proxied by the abundance of one pioneer and one late-successional species on soil C:N:P biogeochemistry. Moreover, the role of the two herbaceous focal species in soil C:N:P accumulation was investigated from the early post-deglaciation stages to the later stages close to the development of an alpine grassland. The study was published as a research article and is reported here in Chapter 2.

Soil carbon stocking of a variety of alpine pastures

Among the several ES provided by alpine grasslands, climate regulation through soil C sequestration is one of the most important (Scharlemann et al., 2014) since it counteracts the increasing amount of CO₂ in the atmosphere related to human activities (Lefèvre et al., 2017). Research on soil C stocks is abundant, dealing with a high variability of different ecosystems (Guo and Gifford, 2002; Liu et al., 2015). However, little is

known about alpine grasslands, both referring to productive vegetation in managed pastoral districts and of more marginal, alpine and subnival plant communities. Among alpine grasslands, ecological conditions differ according to environmental and biological gradients. Altitude, topography, geological substrate, and climate interact with biotic components and determine species composition of plant communities; however, the role of all these abiotic and biotic factors on C sequestration in alpine grasslands is almost unknown.

The second specific objective of the present thesis was to evaluate the relative importance of environmental (topography and climate) and biotic (plant species composition) factors in explaining soil C stocks over a large sample of alpine grasslands. Studied grasslands encompassed a broad variability of alpine summer pastures, from nival and subnival vegetation to intermediate and thermophilic ones, scattered over the entire western Italian Alps. The study was published as a research article and is reported here in Chapter 3.

Factors affecting alpine grasslands forage provisioning service

Another well-known ES, which is understudied as well as soil C sequestration, delivered by alpine pastures is the production of high-quality forage. There are two main features related to the provisioning service of forage which deserve to be studied in detail: biomass productivity and forage quality for livestock nutrition. Biomass productivity is one of the main goals of any farming system and the biotic and abiotic factors able to increase it, also through modifications in species composition, have been studied for centuries. More recently, it has been highlighted that the chemical composition of forage influences ruminant metabolism and contributes to satisfy livestock needs. Forage quality is generally assessed through standardised chemical analyses or near infrared techniques (based on a set of chemical analyses) in order to obtain the proximate composition, i.e. the content of specific components such as crude protein, soluble sugar, and fibre fractions. Elevation, slope, temperature, and precipitation interact with each other and affect grassland forage yield and quality (Dumont et al., 2015; Dongdong et al., 2020). Additionally, the extremely diverse plant species composition of alpine pastures influences the quality of the forage resource, with relevant variations throughout the vegetative season, due to plant phenological advancement (Jeangros et al., 1999; Andueza et al., 2016; Ravetto Enri et al., 2017). Only in the Western Italian Alps Cavallero et al. (2007) described more than 90 different grassland types and hundreds of different pastoral facies.

Previous studies have focused on the effects of individual factors on forage productivity and quality, especially under artificially manipulated conditions (Dumont et al., 2015). Other studies focused on the effects on temporary low-lying species-poor grasslands or in meadows (Andueza et al., 2016). However, knowledge about the simultaneous effects of these drivers and, particularly, of their relative importance on forage yield and proximate composition of species-rich alpine pastures is still limited.

The third objective of the thesis was to assess the relative importance of topographic, climatic and vegetation-related (such as the cover of functional groups of species and plant phenological stage) variables on the forage production and quality of alpine pastures. We compared six different grassland types distributed over an altitudinal-fertility gradient within an endalpic alpine valley of the Western Italian Alps (Gran Paradiso National Park). The study was submitted to a Grass and Forage Science ISI journal as a research article and it is reported here in Chapter 4.

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2. Towards alpine grassland: plant-soil interactions along proglacial primary succession

Extended paper title: Successional herbaceous species affect soil processes in a high-elevation alpine proglacial chronosequence

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Abstract

The study investigated plant-soil interactions along a proglacial chronosequence in the Italian Alps, with a specific focus on pioneer and grassland species structure and biogeochemical processes, with the aim to evaluate the biotic patterns in ecosystem development. We recorded vascular plant frequencies and the mean diameter of one pioneer and one grassland target species in 18 permanent plots distributed along six different stages encompassing a 170-years chronosequence in the Lauson Glacier forefield (NW Italy). We evaluated the main soil properties and measured the C:N:P stoichiometry in the biomass of pioneer and grassland target species and in the underlying soil. For comparative purposes, we analysed also bare soils sampled near the sampled plant individuals. Pioneer species number and cover significantly increased 10 and 40 years after deglaciation respectively, while alpine grassland species cover and number peaked only after 65 and 140 years, respectively. Along the chronosequence, soils beneath vascular plants were enriched in nutrients, especially under individuals of alpine grassland species, with total organic C contents ranging between 1.3 and 8.9 g·kg⁻¹ compared to 0.2 and 3.3 g·kg⁻¹ in bare soils. Nitrogen content in bare soils was nearly undetectable, while it increased in the plant-affected soils, leading to a more balanced C:N:P stoichiometry in the oldest stages. The colonisation of alpine grassland species started immediately, although species number and cover increased only when the soil acquired sufficient nutrient supply and functionality. Although the ecosystem remained C and N limited, the soil could provide adequate conditions for more competitive species establishment, as confirmed by the increasing number and cover of alpine grassland species. Thus, soil nutrient dynamics were strongly influenced by plants, with a major influence triggered by late-successional grassland species.

Keywords: biotic and abiotic processes, carbon, nitrogen, phosphorus, plant-soil interaction

Introduction

Throughout the last 170 years, the alpine region has been affected by an enhanced glacier retreat, with the exception of limited periods of glacier advance (Dyurgerov and Meier, 2000; Pörtner et al., 2019). This phenomenon accelerated at historically unprecedented rates during the last few decades, with alpine glaciers that have already lost nearly 50% of their total surface area since 1850 (Paul et al., 2004; Zemp et al., 2006). Consequently, new ice-free surfaces can nowadays provide the opportunity to investigate primary successions, soil development and emerging patterns of ecosystem structure and functions (Matthews, 1992; Egli et al., 2010).

The glacier retreat modifies the hydrological response and the sediment transport within glacier-covered basins, while the new-ice-free areas are destabilized by paraglacial processes. Mineral substrate left free from ice lacks in biological materials and the net primary production is limited by extreme abiotic constraints, such as low temperatures, intense solar irradiation and strong temperature variations (Stöcklin and Bäumler, 1996; Vitousek et al., 1997; Jones and del Moral, 2009). Receding glaciers open up surfaces for the succession of biota, which protects the released detritus. In turn, the stabilized till supports storage and interception of water and elements that allow plant colonization and soil development (Matthews, 1992, 1999; Walker and del Moral, 2003). The combination of these abiotic and biotic processes and their interactions change with time since deglaciation, creating unique chronosequences (Egli et al., 2001; Cannone et al., 2008; Eichel, 2019), characterized by a short space-for-time substitution, from young, recently deglaciated debris to the oldest moraines (Pickett, 1989). Time since deglaciation is indeed assumed to be the key driver for ecosystem development, even though local processes at a small scale are not always negligible (Burga et al., 2010; Dümig et al., 2011).

One of the typical vegetation dynamics in these environments leads to species replacement along successional stages, from pioneer to early-, mid- and late-successional species, where the latter are typical alpine grassland species, above treeline (Eichel, 2019). In order to identify successional trajectories and biodiversity dynamics, the correct attribution of the ecological needs to the species is essential, based on phytosociological findings or species traits. Grouping species in social behaviour types (Bartha et al. 2008; Troiani et al. 2016) and evaluating their patterns along a chronosequence can provide a more comprehensive interpretation of vegetation dynamics and an easier tool

for comparative community ecology (Caccianiga and Andreis, 2004). Additionally, the study of species traits, such as demographic structure of target species belonging to different successional stages (i.e. pioneer or late-successional species) or Competitor, Stress-tolerator, Ruderal (CSR) strategies (Grime, 2006), can allow deep insights into the reproductive mechanisms or the community interactions such as facilitation (Caccianiga et al., 2006; Těšitel et al., 2014).

The progressive plant colonization of high-altitude environments leads to soil formation, including mineral weathering (Mavris et al., 2010; Bernasconi et al., 2011), changes in microbial communities (Nemergut et al., 2007; Jumpponen et al., 2012), carbon (C) accumulation and nutrient cycling, especially nitrogen (N) and phosphorus (P) (Egli et al., 2006; Bernasconi et al., 2011). The combination of pedogenic processes with the C:N:P stoichiometry in the soil-microorganisms-plant system can furnish key information for understanding the ecological relationships between plant communities and nutritional requirements. In particular, pioneer communities can play an essential role in the kick-off of soil biogeochemical processes, while late-successional ones exert a stronger influence on nutrient dynamics (Matthews 1992). It should be further noticed that, in high altitude primary successions, the effect of single herbaceous species may be easily identified, because of the low and discontinuous vegetation cover. Bonanomi et al. (2016), for instance, described the effect of single plants of *Silene acaulis* on soil C and N contents along an altitudinal gradient, proving its beneficial effects compared to soil without vegetation.

Soil nutrient dynamics and ecosystem development may in turn drive the C:N:P stoichiometry in photosynthetic tissues (Sardans et al., 2012; Zhang et al., 2018). If C and N generally remain the limiting factors in alpine ecosystems (Körner, 2003), in proglacial environments, the short spatial-temporal span can lead to faster changes in C:N:P patterns in plant species, although nutrient limitation and co-limitation in these environments are still poorly understood. However, a comprehensive approach which encompasses social behaviour types cover and successional single species dynamics with soil biogeochemistry still remains largely unknown in high-altitude proglacial chronosequences.

Based on these considerations, we hypothesized that the succession and the related actions of plant species occurring in a short spatial-temporal span since deglaciation play a pivotal role for soil formation and development, leading to favourable ecological conditions for progressively hosting more competitive species. Thus, this study aimed

at evaluating pioneer and late-successional grassland species patterns and their role in soil development and nutrient biogeochemistry along a high-altitude proglacial chronosequence in the western Italian Alps (Lauson glacier). To deeply understand the soil-plant interplayed relationship, we further investigated the role of two herbaceous single species in nutrient dynamics, i.e. the pioneer *Saxifraga oppositifolia* L. subsp. *glandulifera* Vacc. and the late-successional *Silene acaulis* (L.) Jacq subsp. *bryoides* (Jord.) Nyman.

Materials and Methods

Study area

The study was carried out in the proglacial foreland of the Lauson glacier, a small glacier with a 0.23 km² surface and 700 m length (Smiraglia and Diolaiuti, 2015) (Figure 2.1), located within Gran Paradiso National Park (SAC/SPA IT1201000) in the upper Cogne Valley (Aosta Valley Region, North-Western Italy). The considered proglacial foreland was between the glacier terminus in 2016 and the frontal moraines left around 1820 during the Little Ice Age, located at 3030 and 2750 m a.s.l., respectively. The linear distance between the two moraines is 1300 m, with a surface of about 0.65 km². The climate of the Cogne Valley is endalpic, with mean annual precipitation of about 700 mm and mean annual temperature of +4.1 °C (mean values of Valnontey and Lillaz weather stations, at 1700 m a.s.l.). The proglacial foreland is usually covered by snow between October and mid-July, and it has mean annual temperatures between -1 and -3 °C (Mercalli and Cat Berro, 2003). The soils are Eutric Skeletic Regosols (IUSS Working Group WRB, 2015), characterized by homogeneous texture and parent rock composition (mainly paragneiss with small quantities of amphibolites, Le Bayon and Ballevre, 2006), with disturbances limited to cryoturbation, solifluction and a weak water erosion. The vegetation is mainly composed of sparse individuals of alpine pioneer and grassland species, such as *Saxifraga oppositifolia*, *Artemisia genipi* Weber ex Stechm., *Silene acaulis* and *Poa alpina* L. Out of the proglacial area, the climax vegetation is alpine grassland, dominated by *Carex curvula* All. The potential treeline in the area is around 2350 m a.s.l. (Pecher et al., 2011). Climax soils under the climax alpine prairie are Skeletic Umbrisols or Skeletic Dystric Cambisols (IUSS Working Group WRB, 2015; D'Amico et al., 2020a).

We retraced the retreat of the proglacial terminus since 1820 until 2016 by analyzing historical field surveys carried out by the *Istituto Geografico Militare* in 1820, 1882, and 1931 and by performing photointerpretation of Regional Technical Maps (1975), ortophotos (1999, 2005, 2012), and SPOT satellite images (2009) (SctGeoVdA, 2020). A six stage chronosequence was then identified, encompassing a temporal range of 170 years and a spatial distance of 1000 m (Figure 2.1), with the lowest limit at 2850 m a.s.l. (Table 2.1), ca. 500 m above potential treeline (according to Pecher et al., 2011). Half of the stages were located within 200 m from the 2016 glacial terminus in order to deeply examine the early phases of the primary succession, i.e. the ones occurred in the last 40 years.

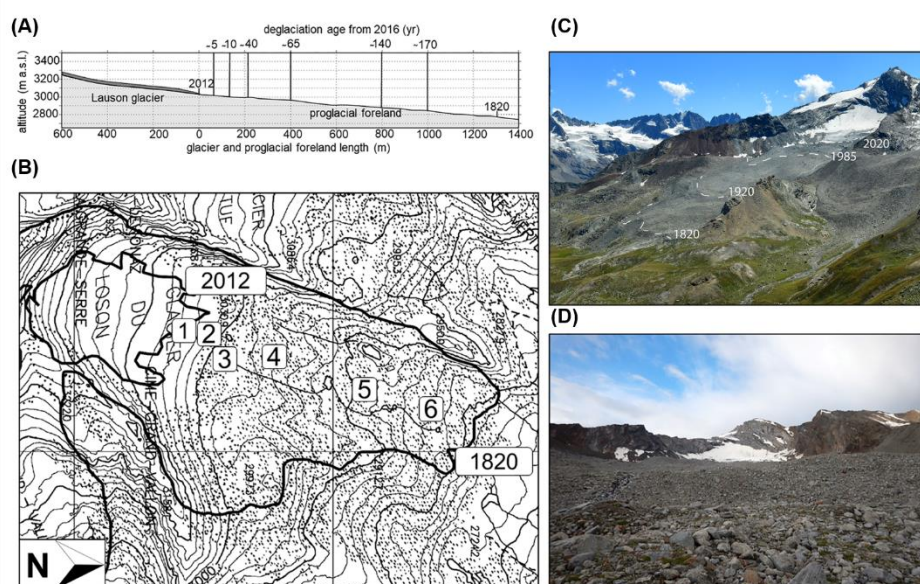


Figure 2.1. Representation of the Lauson glacier foreland: elevation profile (A) including the limits of the reconstructed glacier retreat (1820–2012) and the age from deglaciation of the six stages of the chronosequence; Regional Technical Map (B) with the positions of the stages of the chronosequence and the glacier terminus in 2012 and 1820; photo of the study area (C) with drawing of four known historical glacier terminus; photo of the oldest stage (D) deglaciated for ca. 170 years.

Table 2.1. Description of the identified chronosequence stages.

Chronosequence stage	Deglaciation age in 2016 (yr)	Distance from glacier terminus in 2016 (m)	Altitude (m a.s.l.)
1	~5	~35	3025
2	~10	~90	3015
3	~40	~180	3000
4	~65	~350	2970
5	~140	~800	2885
6	~170	~1000	2850

Vegetation surveys

Three permanent quadrat plots (5 × 5 m) were placed at each chronosequence stage, avoiding areas visibly disturbed by water erosion or deposition processes. Plant species composition was then described following the vertical point-quadrat method (Daget and Poissonet, 1971) at every node of a 25 × 25 cm grid (accounting for a total of 441 sampling points). At each point, all vascular plants were identified at species or subspecies level, while cryptogams were pooled in an aggregated group. A complete list of all occasional species occurring within the plot but not found at the nodes was recorded as well, following the same approach as the phytosociological one (Braun-Blanquet, 1932). The species cover was calculated as its frequency of occurrence across the plot divided by the total number of sampling points. A percentage cover of 0.1 % was attributed to all occasional species not found at the nodes but within the plot (Tasser and Tappeiner, 2005). Taxonomic nomenclature followed the new checklist of the Italian vascular flora (Bartolucci et al., 2018). Plant diversity of vascular plants was assessed for each plot in terms of species richness and Shannon-Wiener index (Magurran, 1988). Moreover, we associated a phytosociological optimum (at class level) to each vascular plant species according to Aeschimann et al. (2004) in order to identify different social behaviour types (hereafter SBTs) (Bartha et al. 2008; Troiani et al. 2016) by aggregating species which are characterized by similar ecological needs. We identified two SBTs, corresponding to different vegetation successional stages: (i) pioneer species (belonging to *Thlaspietea rotundifolii* class) and (ii) alpine grassland species (belonging to

Caricetea curvulae, *Carici rupestris-Kobresietea*, *Elyno-Seslerietea*, *Molinio-Arrhenatheretea*, *Nardetea strictae*, and *Salicetea herbaceae* classes). Following this approach, adopted in many different alpine contexts (e.g. Pittarello et al., 2016; Moris et al., 2017; Perotti et al., 2018), we computed species number and cover for each SBTs in the different plots.

Additionally, we studied the population structure of two target species, *Saxifraga oppositifolia* L. subsp. *glandulifera* Vacc. (hereafter *Saxifraga*) and *Silene acaulis* (L.) Jacq subsp. *bryoides* (Jord.) Nyman (hereafter *Silene*), chosen according to the criteria of abundance and ubiquity along the chronosequence. *Saxifraga* was selected as the pioneer species, with a phytosociological optimum corresponding to *Thlaspietea rotundifolii* (Aeschimann et al., 2004). *Silene* was chosen as an alpine grassland species, with a phytosociological optimum corresponding to *Caricetea curvulae* (Aeschimann et al., 2004). For both target species, we determined the diameter (mean value of the two min and max perpendicular diameters, in cm) of all individuals found in each vegetation plot, as a proxy of individual age (Benedict, 1989). We then assessed the population structure by calculating the frequencies of occurrence (number of individuals in 100 m²) of each 1-cm diameter class.

Soil and plant tissue analyses

A soil profile close to each vegetation plot was opened and described following the FAO guidelines (FAO, 2006). Soil samples were then collected from each genetic horizon, air-dried and sieved at 2 mm. Soil pH was measured potentiometrically in deionized water (soil:water = 1:2.5). Total carbon (TC) and nitrogen (TN) were determined by dry combustion with an elemental analyzer (NA2100, CE Instruments, Rodano, Italia). Carbonate content was assessed by volumetric analysis. The content of total organic carbon (TOC) was determined by difference between TC and carbonate-C.

Amorphous iron oxides (Fe_o) were extracted with an ammonium oxalate solution, buffered at pH 3 (Schwertmann, 1964), while total pedogenic iron oxides (Fe_d) were determined by the dithionite-citrate-bicarbonate extraction (Mehra and Jackson, 2013). Two forms of phosphorus were assessed: total phosphorus (TP), determined following Bowman (1988), and bicarbonate extractable phosphorus (P_{av}), assumed as readily available phosphate for plants (Olsen, 1954). The ammonium acetate extraction method (pH 7) was adopted to determine cation exchange capacity (CEC) (Chapman, 1965); basic cations (Ca, Mg, K) were then

measured by Atomic Absorption Spectrophotometry (AAS, Perkin Elmer, Analyst 400, Waltham, MA, USA).

To evaluate the influence of vegetation on soil properties, in each plot three replicates of *Saxifraga* and *Silene* individuals with the largest diameters were sampled, as well as the underlying soil at 0-10 cm depth. For comparative purposes, three soil replicates without vegetation, close to the eradicated plants, were also collected at each stage.

The eradicated individuals of *Saxifraga* and *Silene* were placed in sealed polyethylene bags, immediately stored at 4°C in a portable refrigerator, and transported to the laboratory, where green stems and leaves were separated. Aboveground green tissues (i.e. stems and leaves) were dried, grounded to 0.5 mm and analyzed to assess total C, N, and P contents following the above-mentioned procedures.

Soil samples were separated in two aliquots: one was air-dried, sieved, and analyzed to determine TOC, TN, TP, and P_{av} as described above. The other aliquot was processed within 24 hours from sample collection, in order to measure microbial biomass C (C_{micr}) and N (N_{micr}). In particular, a 30 g aliquot was extracted with 100 mL K_2SO_4 0.5 M, while a 10 g aliquot was fumigated with chloroform for 18 h before extraction with 50 mL K_2SO_4 0.5 M. The DOC concentration in non-fumigated soil extracts was determined with a TOC analyser (Elementar, Vario TOC, Hanau, Germany) after filtration with 0.45 µm membrane filters). The same procedure was applied to fumigated samples; the difference in DOC between fumigated and non-fumigated samples, corrected by a recovery factor of 0.45, was C_{micr} (Brookes et al., 1985).

In order to measure N_{micr} , ammonium (extractable $N-NH_4^+$) concentrations in soil extracts were determined spectrophotometrically (U-2000, Hitachi, Tokyo, Japan) by the method described by Crooke and Simpson (1971). Nitrate (extractable $N-NO_3^-$) was determined following Cucu et al. (2014). Total dissolved nitrogen (extractable TDN) in the extracts was determined as reported for DOC. Dissolved organic nitrogen (extractable DON) was determined as the difference between extractable TDN and inorganic nitrogen (extractable $N-NH_4^+ + N-NO_3^-$). Microbial nitrogen (N_{micr}) was then calculated as the difference in extractable TDN between fumigated and non-fumigated samples, corrected by a recovery factor of 0.54 (Brookes et al., 1985). All analyses were carried out in triplicate.

Statistical analyses

The differences among the six stages of the chronosequence in terms of the considered vegetation variables (i.e. cryptogam and vascular plant cover, the two plant diversity indices, and species number and cover for the two SBTs) were tested performing a one-way ANOVA. To investigate the variations within the population structures of *Saxifraga* and *Silene* along the chronosequence we performed a PERMANOVA for each species on the frequencies of diameter classes among stages. The similarity index was calculated using Euclidean distance method and 9999 permutations were set.

The soil property changes triggered by *Saxifraga* and *Silene* were analysed with two separate one-way ANOVAs. The same analysis was carried out on chemical properties (i.e. TOC, TN, TP, C:N, and N:P) of *Saxifraga* and *Silene* tissues, among stages and between the two plant species. For univariate tests, assumptions of normality and homoscedasticity were checked with Shapiro-Wilk's and Levene's tests, respectively and, in case of assumption violation, logarithmic and square-root transformations were applied to variables prior to perform the ANOVAs. Whenever normal distribution or homoscedasticity did not occur, even after transformations, we performed the non-parametric Kruskal-Wallis test. Tukey's and Dunn's post-hoc tests were adopted for one-way ANOVA and Kruskal-Wallis, respectively, in case of significant differences.

In order to describe the interactions between soil properties and vegetation cover along the chronosequence, two matrices were arranged: (1) a soil property matrix, with TOC, TN, TP, P_{av} , C_{micr} , and N_{micr} of soil samples without vegetation, and (2) a vegetation matrix, including the covers of cryptogams, total vascular plants, pioneer species, and alpine grassland species. A Mantel test was used to calculate the correlation between the soil and vegetation matrices. A preliminary detrended cross-correlation analysis (DCCA) was performed to assess the lengths of gradients (ter Braak and Smilauer, 1998). The DCCA revealed the presence of short (linear) gradients (< 4 standard deviations) so we performed a redundancy analysis (RDA) between the two matrices (ter Braak and Smilauer, 1998).

Univariate analyses were carried out with SPSS 24 (SPSS, 2016), while PERMANOVA and Mantel test analysis with PAST 3.15 (Hammer et al., 2001) and RDA with CANOCO 4.5 (Ithaca, NY, USA); significance was set at $p < 0.05$.

Results

Vegetation

A total of 65 vascular plants, belonging to 19 botanical families, were recorded within the 18 plots. The most abundant species were *Saxifraga bryoides* L., *Cerastium uniflorum* Clairv., *Silene acaulis* subsp. *bryoides*, *Poa alpina* L., and *Saxifraga oppositifolia* subsp. *glandulifera*. No species belonging to the Fabaceae family were found in the study area. Five years since deglaciation, seven species colonised the siliceous parent material of the Lauson foreland and the pioneer *Saxifraga oppositifolia* was the most widespread in terms of both frequency and cover. Vegetation cover increased significantly along the chronosequence, for both cryptogams and vascular plants (Figures 2.2a and 2.2b). In particular, vascular plant cover increased from values close to 0 at 5-10 years since deglaciation to 24 % at the 170-year stage (Figure 2.2b). Species richness and Shannon-Wiener index increased along the chronosequence as well (Figure 2.2c and 2.2d).

The number of species belonging to both SBTs increased along the chronosequence as well (Figures 2.3a and 2.3b). In particular, pioneer species number significantly increased already after 10 years and, even if not statistically significant, tended to decline at older stages, while alpine grassland species number showed a slower but progressive increase along the whole chronosequence. Species cover significantly differed among stages for both pioneer and alpine grassland species, reaching the highest values since 40 and 65 years after deglaciation, respectively (Figure 2.3c and 2.3d).

Overall, we studied 1931 plant individuals for the population structure analysis, 775 were *Saxifraga* (observed in 14 plots out of 18) and 1176 *Silene* (observed in 12 plots out of 18).

In the 5-year deglaciated plots, many *Saxifraga* individuals (ca. 70 in 100 m²) were counted, with the highest frequencies in the 1-cm diameter class (Figure 2.4a). The highest number of individuals and cover was found in plots deglaciated for 40 years, with plants occurring in all diameter classes up to 25 cm and abundance of large individuals (mean diameter 13 cm and several individuals with diameter over 30 cm). This species almost disappeared in plots deglaciated for longer times. Conversely, no individuals of *Silene* were found within the first deglaciation stage, while it sparsely colonized young moraines only after 10 years (Figure 2.4b). The species became more frequent after 40 years (mainly with small individuals) and spread on the 65 years-old

areas, with diameter classes up to 19 cm constantly present. In the last two stages, the frequencies of regenerating individuals (1- and 2-cm classes) doubled and large individuals (45-cm class) were detected.

According to PERMANOVA results, the distribution frequency of individual diameters differed among the chronosequence stages for both target species (Figure 2.4).

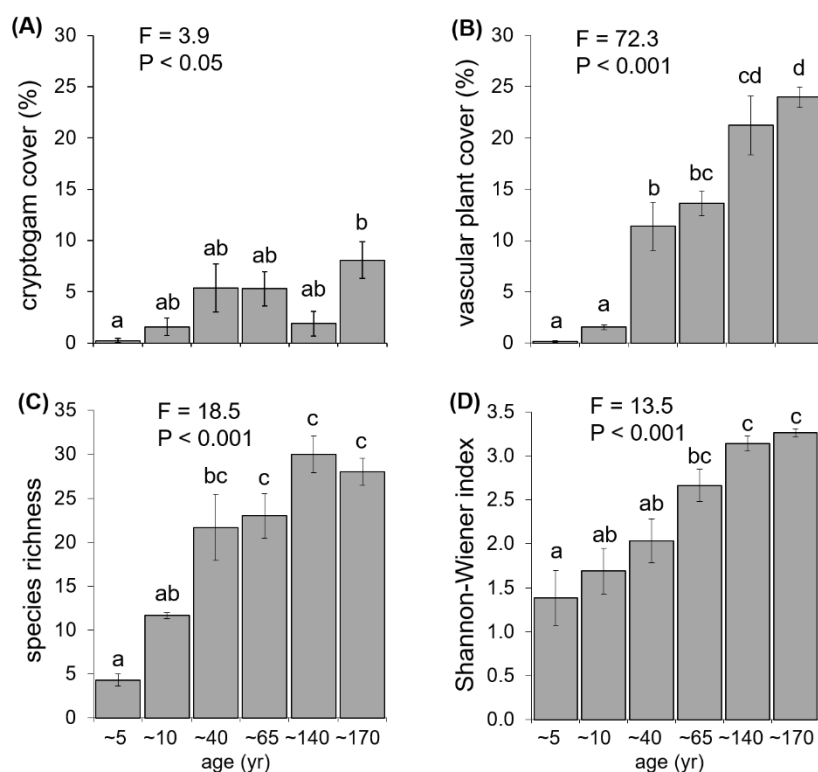


Figure 2.2. Plant species cover ((A), cryptogams; (B), vascular plants) and diversity indexes ((C), species richness; (D), Shannon-Wiener index) along the six stages of the chronosequence. Different letters indicate significant differences ($p < 0.05$) among stages according to Tukey's HSD test.

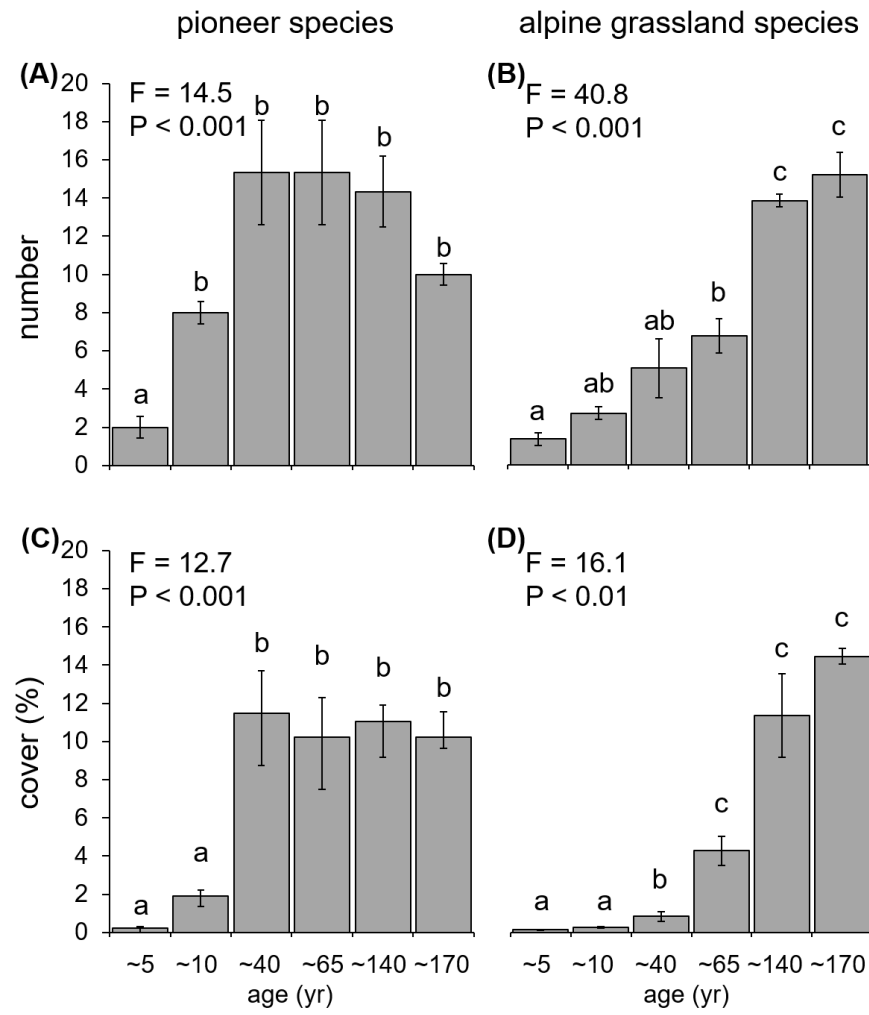


Figure 2.3. Species number and cover for the two social behaviour types along the six stages of the chronosequence: pioneer species (A,C) and alpine grassland species (B,D). Different letters indicate significant differences ($p < 0.05$) among stages according to Tukey's HSD test.

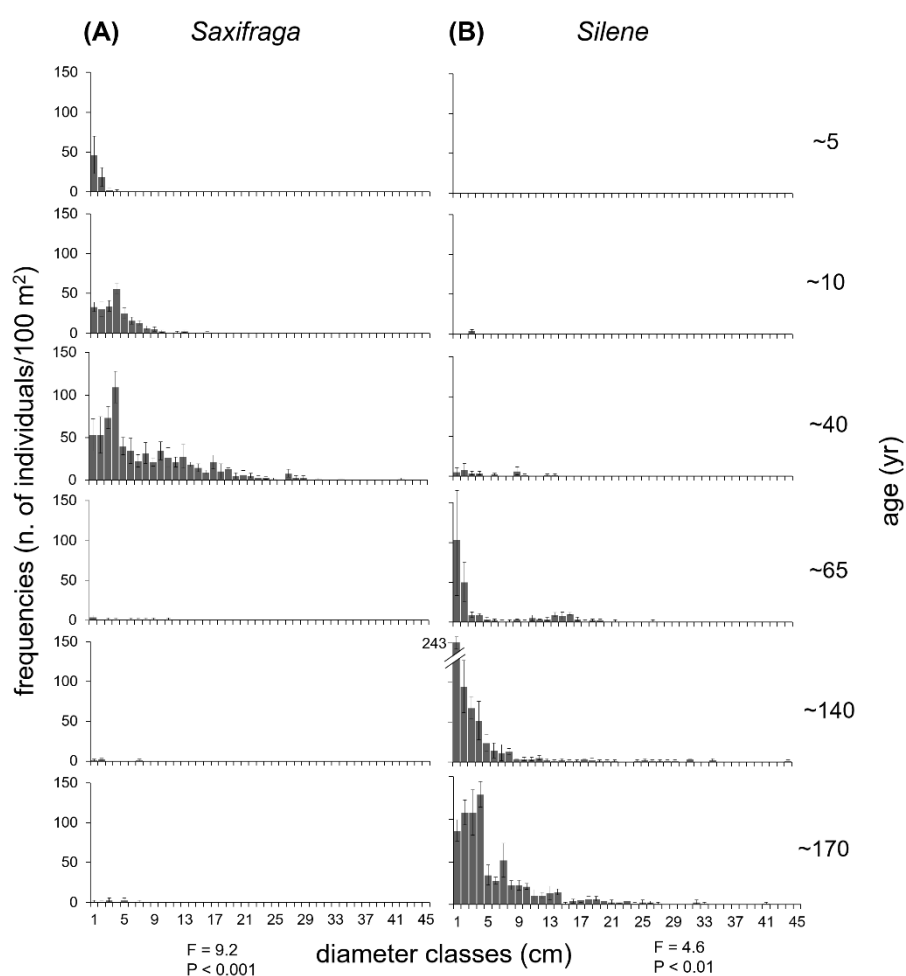


Figure 2.4. Population structure (distribution frequencies of individual diameters) in each stage of the chronosequence for the two target species *Saxifraga oppositifolia* L. subsp. *glandulifera* Vacc. (A) and *Silene acaulis* (L.) Jacq. subsp. *bryoides* (Jord.) Nyman (B). *Silene* individuals were not found in the first stage (~5 years) and are not represented. F and p indicate the results of PERMANOVA analysis among stages and within species.

Soil development

According to the WRB classification (IUSS Working Group WRB, 2015), the soils of the first and third stages of the chronosequence were classified as Eutric Skeletic Regosols, while the others as Eutric Skeletic Regosols (Turbic). Soil chemical properties are shown in Table 2.2. We observed two to five genetic horizons in the soil pits of each stage, including A, AC, CA, and C horizons, with soil depths (A+AC or CA horizons) ranging from 15 to over 40 cm. Soil pH values ranged from 8.9 (C horizon deglaciated for 10 years) to around 6.0 in the upper horizon of the 170-years old stage. pH values decreased below 7.0 only in the surface horizons of the 65 years-old stage. Despite the high pH values, no carbonates were detected. Total organic carbon (TOC) was always greater in surface than in deep soil horizons and increased along the chronosequence, with a maximum content of 26.2 g kg⁻¹ in the A1 horizon deglaciated for 170 years. Organic horizons were never detected. Total nitrogen (TN) was below the limit of quantification in soils up to 40 years since deglaciation and in all C horizons of the chronosequence (except the 140 years-old one), while the greatest contents were detected in A horizons, ranging between 0.2 and 1.5 g kg⁻¹. As a consequence, the TOC:TN ratio varied between 8 (at 40 years) and 17 (at 170 years).

Younger soils (i.e. up to 40 years) showed higher Fe_o concentrations than older ones and both Fe_o and Fe_d were higher in surface horizons than in deeper ones. The Fe_o:Fe_d ratio, which indicates the ratio between poorly crystalline Fe (hydr)oxides and pedogenetic Fe (hydr)oxides, decreased along the chronosequence with the lowest value in the soils deglaciated for 170 years, in A2 and AC horizons (0.4 g kg⁻¹). Total phosphorus (TP) ranged between 593 and 776 mg kg⁻¹ without recognizable age or depth trends, whereas the available form (P_{av}) was 0.5 mg kg⁻¹ in the youngest soil stages and reached 4 mg kg⁻¹ in the A horizons of the 170 years-old stage. Cation-exchange capacity (CEC) ranged between 0.89 cmol⁽⁺⁾ kg⁻¹ in the C horizon of the 65 years-old stage and 10.1 cmol⁽⁺⁾ kg⁻¹ in the oldest topsoil (Table 2.3). Base saturation (SATB) was greater in younger stages, ranging between 67% and 100% in the first 40 years-old stages. In the oldest stages, it was generally lower (except for A horizon from the 65 years-old stage with 83%) with a minimum value of 23.7% in the AC horizon of the 140 years ice-free stage. Calcium ion was the main element saturating the exchange complex, both in terms of concentration and ratio, especially in deeper soil horizons (Table 2.3).

Table 2.2. Chemical properties of soil pits along the six stages of the chronosequence. pH; TOC, total organic carbon; TN, total nitrogen; Fe_d, pedogenic iron oxides; Fe_o, iron amorphous oxides; Fe_o:Fe_d, poorly crystalline to pedogenic iron oxide ratio; TP, total phosphorus; P_{av}, bicarbonate extractable (available) phosphorus.

Age yr	Horizon	Depth cm	pH	TOC g kg ⁻¹	TN g kg ⁻¹	TOC:TN	Fe _o g kg ⁻¹	Fe _d g kg ⁻¹	Fe _o :Fe _d	TP mg kg ⁻¹	P _{av} mg kg ⁻¹
-5	CA	0-5/10	8.5	0.3	0	-	1.6	1.9	0.8	592.9	0.8
	C	5/10-35+	8.3	0	0	-	1.9	2.0	1.0	671.4	0.5
-10	CA	0-3	7.7	0.3	0	-	0.8	1.6	0.5	643.2	0.7
	C	3-15+	8.9	0.2	0	-	1.3	1.7	0.8	700.0	0.5
-40	A	0-3	7.1	1.6	0.2	8.0	1.4	2.8	0.5	727.8	1.1
	CA	3-14	7.4	0.2	0	-	1.7	2.3	0.7	775.6	0.9
	C	14-20+	7.3	0	0	-	1.8	2.3	0.8	705.6	0.7
-65	A	0-4	6.2	8.1	0.6	13.5	1.2	2.7	0.4	713.5	3.5
	CA	4-15	6.9	0.1	0	-	1.0	1.8	0.5	699.6	1.4
	C	15-22+	6.9	0.1	0	-	0.5	1.1	0.5	691.9	0.7
-140	A	0-5/8	6.2	14.1	0.9	15.7	1.1	2.7	0.4	688.4	3.4
	AC	5/8-18/20	6.8	0.7	0.1	-	0.9	1.9	0.5	751.2	0.9
	C	18/20-40+	7.4	0	0	-	0.9	1.6	0.5	605.9	0.7
-170	A1	0-3	6.0	26.2	1.5	17.5	1.0	2.5	0.4	724.4	4.0
	A2	3-10	6.0	11.3	0.8	14.1	0.8	2.0	0.4	728.6	2.8
	AC	10-15	6.4	0.5	0	-	0.7	1.7	0.4	683.4	0.8
	AC/C	15-25/30	7.1	0	0	-	0.7	1.7	0.4	648.7	0.7
	C	25/30-40+	7.4	0.5	0	-	0.7	1.7	0.4	609.9	0.6

Table 2.3. Cation-exchange capacity and base saturation of soil pits along the six stages of the chronosequence. CEC, cation-exchange capacity; Mg_{ex} , magnesium exchangeable cations; Ca_{ex} , calcium exchangeable cations; K_{ex} , potassium exchangeable cations; SATB, base saturation; satMg, magnesium saturation; satCa, calcium saturation; satK, potassium saturation; Ca:Mg, calcium to magnesium ratio; Mg:K, magnesium to potassium ratio.

Age yr	Horizon	CEC cmol(+)kg ⁻¹	Mg_{ex} cmol(+)kg ⁻¹	Ca_{ex} cmol(+)kg ⁻¹	K_{ex} cmol(+)kg ⁻¹	SATB %	sat Mg g kg ⁻¹	sat Ca g kg ⁻¹	sat K g kg ⁻¹	Ca:Mg	Mg:K
-5	CA	-	-	-	-	-	-	-	-	-	-
	C	2.00	0.11	1.23	0.20	77.00	5.50	61.50	10.00	11.18	0.55
-10	CA	1.29	0.05	0.89	0.04	75.61	3.54	69.05	3.02	19.51	1.17
	C	1.53	0.07	3.93	0.10	100.00	4.58	87.14	6.54	56.14	0.70
-40	A	-	-	-	-	-	-	-	-	-	-
	CA	1.18	0.07	0.73	0.05	72.33	5.96	62.12	4.25	10.43	1.40
	C	1.67	0.09	0.92	0.10	66.69	5.51	54.98	6.20	9.98	0.89
-65	A	2.67	0.18	1.94	0.11	83.36	6.79	72.51	4.07	10.69	1.67
	CA	2.05	0.07	0.76	0.10	45.52	3.27	37.15	5.09	11.34	0.64
	C	0.89	0.04	0.44	0.05	59.31	4.34	49.47	5.50	11.41	0.79
-140	A	7.36	0.26	2.36	0.12	37.23	3.49	32.04	1.69	9.18	2.06
	AC	4.11	0.09	0.84	0.04	23.67	2.28	20.42	0.97	8.96	2.34
	C	1.36	0.07	0.66	0.09	60.29	5.15	48.53	6.62	9.43	0.78
-170	A1	10.08	0.34	2.16	0.18	29.40	2.78	25.21	1.41	6.31	1.88
	A2	7.13	0.19	1.26	0.10	24.31	1.63	21.81	0.87	6.63	1.88
	AC	0.99	0.06	0.53	0.06	65.54	6.17	53.78	5.60	8.72	1.10
	AC/C	0.96	0.05	0.54	0.06	68.00	4.98	56.60	6.41	11.36	0.78

Soil and plant interaction

Chemical composition in the topsoil layers sampled under *Saxifraga* (SaxS), *Silene* (SilS) and in the corresponding non-vegetated soils (BareS) significantly differed within the same age and among stages (Figure 2.5). The comparisons among all the three target soils were possible only at the third and fourth stages, where we found individuals of both *Saxifraga* and *Silene* with adequate development. Total OC showed a lag time in the first stages and then increased, especially with *Silene* establishment, reaching 6-8 g C kg⁻¹ after 140 years, whereas the C content in the non-vegetated soil reached no more than 4 g C kg⁻¹ (Figure 2.5a). Total N followed the same trend with more pronounced differences between the vegetated and non-vegetated soil samples (Figure 2.5b). At the 170 years-old stage SilS showed the highest N content. The stoichiometric TOC:TN ratio did not differ among target soils nor among stages, except for a higher value of SilS compared to BareS at the fifth stage (Figure 2.5c). Microbial C and N in vegetated and non-vegetated soils was comparable in the youngest stages and then significantly increased along the chronosequence in SaxS and SilS (Figures 2.5d and 2.5e). Total phosphorus content did not show significant trends in the three series of soils, while an increasing nutrient availability along the chronosequence, due to the presence of the two species, was observed (Figure 2.5f and 2.5g). Lower P_{av} concentrations were found in BareS if compared to SaxS at 10 years since deglaciation and to SilS at 140 and 170 years since deglaciation, respectively.

In plant tissues, a decreasing trend occurred in P and N with time for *Saxifraga* and *Silene*, respectively, leading to a corresponding significant N:P and C:N increase (Figure 2.6). No differences were found between the two target species for any of the considered chemical features at the third and fourth stages, i.e. where both species were found.

A significant correlation was detected between the soil and vegetation matrices by Mantel test ($r = 0.45$, $P < 0.001$), highlighting that chronosequence stages with similar soil properties had similar vegetation covers. Significant correlations between soil and vegetation variables were observed (Figure 2.7), explaining 74.2% of the distribution fitting with the first axis and 2.8% with the second axis. Cryptogam cover appeared weakly associated with soil properties, as highlighted by the arrangement of the arrow relatively to the soil ones. Pioneer species cover showed an intermediate trend between cryptogam and vascular plant covers, this latter being strongly related to TN, C_{micr}, and N_{micr}. Alpine grassland species cover was, instead,

strongly associated with TOC and P_{av} . The only variable arranged in the left part of the bi-plot was TP, showing a contrasting distribution compared to most of the other variables. The chronosequence stages separated well along the two axes of the bi-plot. More specifically, the first two stages were at the opposite of both soil and vegetation features, while the two intermediate stages were mostly related to the covers of cryptogam and pioneer species and the oldest ones related to more developed soils (in terms of TOC and P_{av}) and to late-successional species.

Discussion

The univariate and multivariate analyses highlighted a clear pattern of progressive soil development and vegetation successional dynamics throughout the six stages of the Lauson proglacial foreland, at increasing ages from deglaciation. More specifically, the colonization patterns along the chronosequence of the foreland by vegetation, considering the large difference in elevation between the lower limit of the study area and the potential treeline (500 m), was extremely rapid in the first forty years following deglaciation, in terms of both species richness and cover. An average of four and twelve different species were able to colonize the Lauson proglacial till after 5 and 10 years since deglaciation, respectively. This early process was more rapid than the one observed in the Austrian Alps by Tscherko et al. (2005) and Raffl et al. (2006), in study areas located around the potential treeline (study areas at 2300-2450 m a.s.l., with a potential treeline at 2400 m a.s.l. according to Pecher et al., 2011). Conversely, the studied area was comparable to the results obtained by Burga et al. (2010) in Switzerland, in a proglacial area located at 1900-2100 m a.s.l., i.e. completely below the potential treeline, which is located at 2450 m a.s.l. (Pecher et al., 2011). Similar results were also obtained by Cannone et al. (2008) in the Italian Alps, in a study area located at 2700-2850 m a.s.l., 300-450 m above the potential tree line, located at 2400 m a.s.l. (Pecher et al., 2011), and by Matthews and Vater (2015) in southern Norway (study area at 1420 m a.s.l., 400 m above the local tree line). In all these environments, substrate stability, together with the ability of seeds to reach colonization sites, created a suitable environment for the establishment of pioneer species. The lack of seeds, stated by several studies as a fundamental limiting factor (Chapin et al., 1994; Jones and del Moral, 2009), probably was not the major constraint for plant colonization in the young Lauson foreland, likely because of the short distance between bare sites, freshly released by the glacier, and plant communities growing on nearby slopes, which acted as seed sources. We suggest that, under the

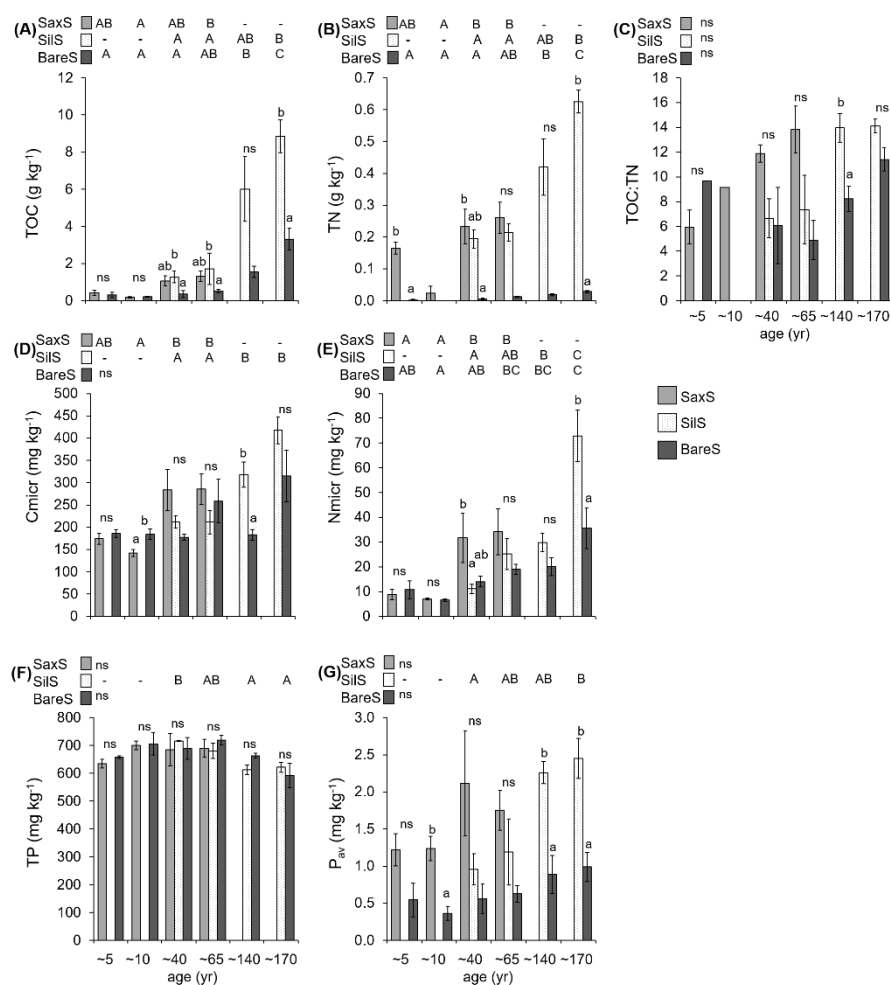


Figure 2.5. Chemical properties of target soils along the six stages of the chronosequence. SaxS, soil under individuals of *Saxifraga oppositifolia* L. subsp. *glandulifera* Vacc.; SilS, soil under *Silene acaulis* (L.) Jacq subsp. *bryoides* (Jord.) Nyman; BareS, bare soil; TOC, total organic carbon (A); TN, total nitrogen (B); TOC:TN, total carbon to nitrogen ratio (C); C_{micr}, microbial carbon (D); N_{micr}, microbial nitrogen (E); TP, total phosphorus (F); P_{av}, bicarbonate extractable (available) phosphorus (G). Different letters indicate significant differences (p < 0.05) among stages within each target soil (uppercase letters) and among target soils within each stage (lowercase letters) according to Tukey's HSD test. ns, p ≥ 0.05.

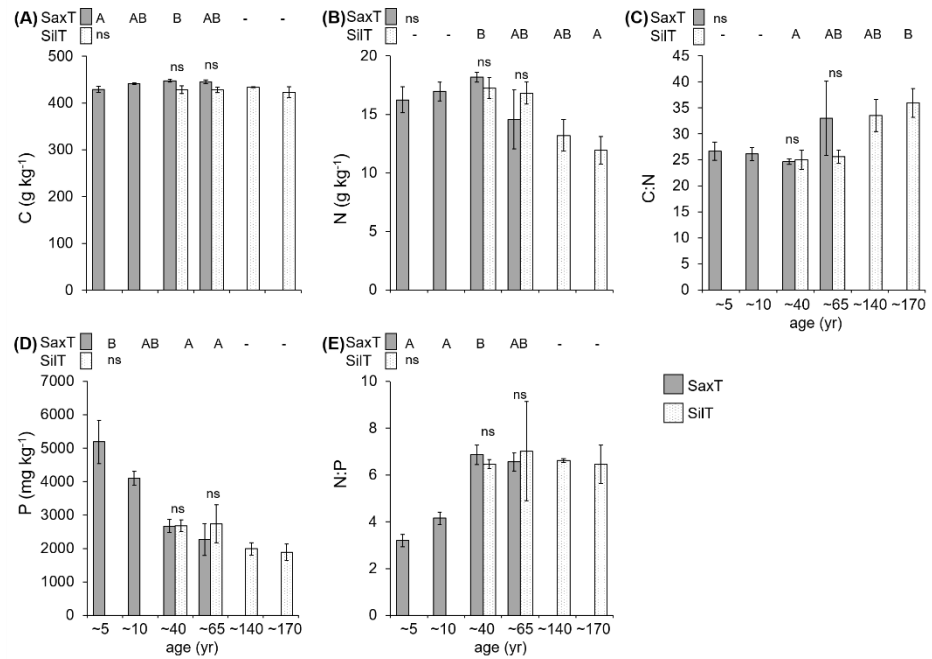


Figure 2.6. Chemical properties of plant tissues for the target species along the six stages of the chronosequence. SaxT, *Saxifraga oppositifolia* L. subsp. *glandulifera* Vacc. L. tissues; SilT, *Silene acaulis* (L.) Jacq subsp. *bryoides* (Jord.) Nyman tissues; C, carbon (A); N, nitrogen (B); C:N, carbon to nitrogen ratio (C); P, phosphorus (D); N:P, nitrogen to phosphorus ratio (E). Different letters indicate significant differences ($p < 0.05$) among stages within each target species (uppercase letters) and between target species within each stage (lowercase letters) according to Tukey's HSD test. ns, $p \geq 0.05$.

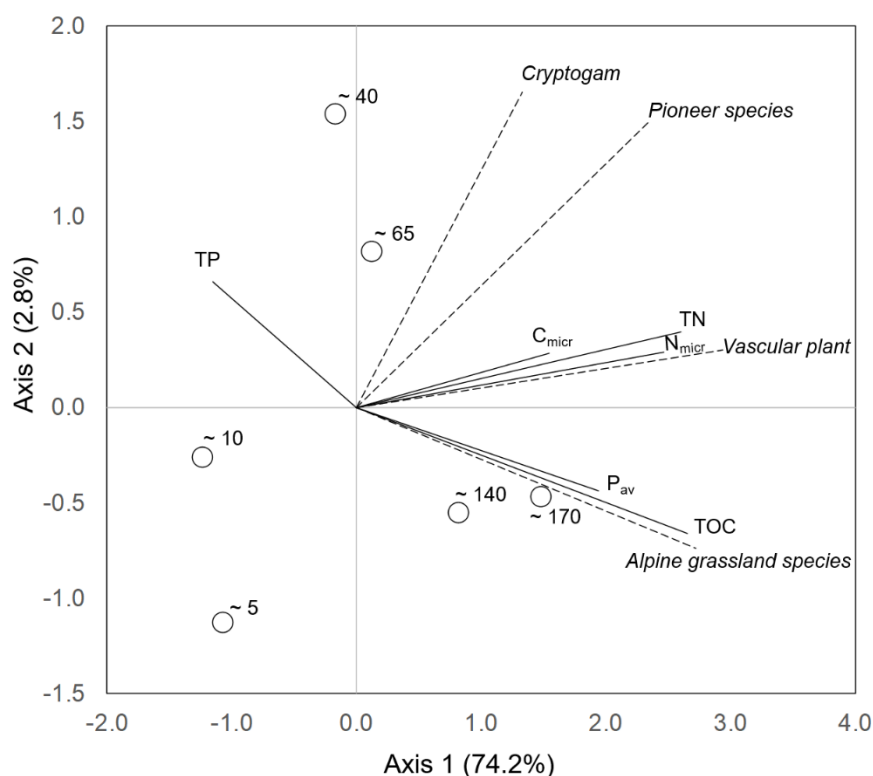


Figure 2.7. RDA ordination bi-plot showing the distribution of the six chronosequence stages (represented by the centroids of the three replicates per stage) and the relationships between soil properties (solid lines) and vegetation covers (dashed lines). TOC, total organic carbon; TN, total nitrogen; C_{micr}, microbial carbon; N_{micr}, microbial nitrogen; TP, total phosphorus; P_{av}, bicarbonate extractable (available) phosphorus. The variance explained by each axes is provided in brackets.

studied conditions, other factors, such as drought, frost and cryoturbation may have played a major role limiting plant establishment, according to Erschbamer and Caccianiga (2016). These factors are naturally interrelated with proglacial micro-topography and with the occurrence of protected microsites, important also for nutrient accumulation. In the Lauson chronosequence, after 65 years since deglaciation, vegetation cover increased due to the additive contribution of the alpine grassland species that partially replaced pioneer ones, contributing to an overall rise in vascular plant cover. Despite the increase in species richness, the vegetation cover was very scarce even after 170 years since deglaciation. At the last stage of the chronosequence, cryptogams and vascular plants indeed occupied only 34% of the surface, while Schumann et al. (2016) recorded mean vegetation cover values of 70% in 123 years-old stages from 16 proglacial forelands in the Alps (located between 2000 and 2600 m a.s.l.). This difference may be related to the complete absence of trees and shrubs within and around Lauson foreland, which is far above the treeline.

The dynamics observed for pioneer and alpine grassland species were confirmed by the population structure of the two target species, *Saxifraga* and *Silene*. In particular, *Saxifraga* showed a typical pioneer behaviour, spreading over the study area since the very first stages of the chronosequence and drastically reducing its cover after 65 years, while the more nutrient-demanding *Silene* firmly established only after (40-)65 years of ice-free development, indicating a complementary successional pattern. Nevertheless, both species showed an uneven-aged demographic structure, with higher frequencies in the smallest diameter classes and lower frequencies in the largest ones. *Saxifraga* and *Silene* seem indeed to perform ruderal strategies (Grime CSR theory, 2006), which implies a great amount of seed production, resulting in the abundance of seedlings and showing fast-colonization ability, rather than a stress tolerant behaviour, as it can be expected in extreme environments such as glacier forelands. The results obtained by our demographic approach, indicating a huge investment in plant reproduction, align with the findings of many authors in proglacial environments, where ruderal strategies allow for plant colonization in the early successional stages (Tscherko et al., 2005; Caccianiga et al., 2006; Gobbi et al., 2010; Erschbamer and Caccianiga, 2016). Frequency variations in diameter classes were statistically significant for both species throughout the entire chronosequence even if a complete transformation of the demographic structure, from uneven- to even-aged, was not reached in the Lauson glacier foreland.

A clear pattern of a primary succession was observed in both SBTs dynamics and target species population structure, with an increase in alpine grassland species number and cover over time, and a simultaneous decline in pioneer species. Overall, considering the limited vegetation cover and the partial plant community substitution among successional stages, the Lauson chronosequence time span (170 years) was not sufficient for the establishment of a stable alpine grassland climax community (highlighted also by the *Silene* demographic structure), supporting the 500-years-minimum age required for *Carex curvula* All. climax type stated by Andreis et al. (2001).

Although all soils found in the Lauson glacier foreland referred to the WRB group of Regosols, we observed clear soil-forming processes such as a weak mineral weathering (evidenced by the Fe_o and Fe_d values) and leaching processes (evidenced by pH and SATB decrease), mostly guided by the soil organic matter build-up with time since deglaciation. The decline observed in pH followed the typical pattern of the proglacial chronosequences (Messer, 1988; Frenot et al., 1998; Anderson et al., 2000); it was however much slower than in proglacial areas located at lower elevations (e.g. D'Amico et al., 2014), in which the overall ecosystem productivity was enhanced by higher temperatures and the larger input of plant litter accelerates soil acidification. In our study, soil pH was very high in the recently exposed sediments. As no carbonates were detected, the high pH was probably related to the initial weathering of silicates, which could lead to a release of base cations, able to increase pH values in very coarse-grained soils. In young ice-free till (ca. 5-10 years from deglaciation), not yet vegetated, these processes can lead to very high pH values because of the lack of colloidal buffer surfaces, as deduced by the very low clay content ($<2\%$) and the related scarce cation exchange capacity (max $2\text{ cmol}^{(+)}\text{ kg}^{-1}$ in CA horizon in the 5 years old material) (Celi et al., 2013). Moreover, the influence of seasonal glacial runoff cannot be excluded, possibly bringing high Ca and K loads, regardless of bedrock (Anderson et al., 1997, 2000) and thus increasing soil pH. High concentrations of K in glacial melt waters, derived from leaching of interlayer cations from biotite, were observed in many works (Drever and Hurcomb, 1986; Stallard, 1995). However, soil acidification occurred over time, likely induced by the increasing vegetation cover and the related release of carboxylic acids through root exudates and/or acidic compounds formed during organic matter decomposition, as well as by organic acids released by bacteria and fungi (Brunner et al., 2011). The leaching of base cations, due to the lack of exchanging surfaces, could contribute as well to the pH decrease (Burt and Alexander, 1996; Darmody et al., 2005; Bernasconi et al.,

2011).

In addition to climatic stress such as drought, frost and cryoturbation, nutrient limitation plays a fundamental role in controlling plant establishment and emphasizes the role of safe-sites (*sensu* Harper et al., 1961), where water fluxes increase moisture and nutrient accumulation, enabling the vegetation to survive. Glacial runoff, which represents an important input of nutrients and base cations, could have facilitated the uptake by the early-successional species such as *Saxifraga*, despite the very harsh substrate of the recently deglaciated debris (Göransson et al., 2016). In the Lauson foreland, we indeed found an optimal base saturation for plant establishment in the first 40 years since deglaciation, with Ca:Mg:K stoichiometric ratios suitable for plant nutrition. Despite the decreasing pH along the terrain age gradient, cation-exchange capacity (CEC) raised, likely as a consequence of organic matter accumulation rather than formation of secondary minerals having higher CEC compared to the unweathered parent material (Bernasconi et al., 2011).

Total nitrogen levels were extremely low and were detectable only in the more organic matter-rich and developed upper horizons. This result highlighted that N was one of the major limiting factors of the Lauson soil-vegetation system due to the lack of N-fixing plants (Körner, 2003; Göransson et al., 2016) and to a possible, moderate contribution of N-fixing free-living microbes (Duc et al., 2009). Göransson et al. (2016), in the wetter Damma proglacial chronosequence in Switzerland, found an exponential increasing trend of TN during the first 137 years of soil development and argued that the main N input was probably due to atmospheric deposition (assumed to be approximately 5 to 10 kg ha⁻¹yr⁻¹). Although in nearby areas (Indren Glacier, Lys Valley, Monte Rosa Group), the atmospheric N deposition was similar, being 6.6 kg ha⁻¹yr⁻¹ in the last few years (Colombo et al., 2019), the smaller N inputs in our soils were associated with lower mean yearly precipitation because of the isolated position of the Lauson proglacial area, surrounded by high mountains. Thus, our findings suggest that in the Lauson foreland, similarly to areas with low N-deposition like Glacier Bay in Alaska or Franz Josef Glacier in New Zealand (Chapin et al., 1994; Menge and Hedin, 2009), the role of atmospheric deposition was less important in N cycling. Furthermore, Göransson et al. (2016) found, particularly at early stages, that N inputs exceeded plant uptake, and low P levels limited plant colonization more than low N levels. In the entire Lauson chronosequence, soil TP contents ranged between 600-700 mg kg⁻¹, which represent a favourable range for P cycling and plant

establishment (Yang et al., 2013). With time, the release of protons and carboxylic acids caused the dissolution of P-bearing minerals, slightly contributing to feed the available P pool and then plant uptake (Celi et al., 2013). In the older, more structured, and more functional soils, with increased cover of alpine grassland species, P biocycling became particularly evident. Particularly at the fourth and sixth stages of the chronosequence, the upper soil horizons became enriched in TP content. This depth trend can be attributed to plant root exploration and uplift of P from the deeper soil horizons to the surface, through deposition of plant residues. However, compared to other proglacial chronosequences in the Alps, with similar time span, the pedogenic processes remained at an incipient stage, likely because of the lower biomass inputs (D'Amico et al., 2014): the cold temperatures characterizing the Lauson forefield and the associated processes (i.e. short growing season, cryoturbation, root damages and slow decomposition rates) slow down plant colonization, which in turn reduces TOC accumulation and N availability; the low N availability, in a low-N deposition site, in turn, slows down plant colonization, creating a negative feedback which inhibits ecosystem development.

The present study provided novel information concerning the differing function of pioneer and late-successional herbaceous species in affecting soil biogeochemistry in recently deglaciated debris. Indeed, the comparison among soils sampled under plants (SaxS and SilS) and non-vegetated soils (BareS) highlighted the pivotal role of vegetation in soil development and nutrient mobilization, along the whole chronosequence, from the very early stages to the latest ones. *Silene* performed a greater soil conditioning than *Saxifraga* in terms of TOC and TN accumulation and development of microbial biomass even within the early stage time points of soil development where both plant species occurred. This may be due to the different growth forms of the two target species, as the cushion species *Silene* may exert more enhancing effects on soil formation than the prostrate species *Saxifraga* (Bonanomi et al., 2016). The drastic decline of *Saxifraga* after 65 years in the chronosequence, likely induced by the competition with more nutrient-demanding species, suggested a facilitation process for the establishment of other plants, linked to the several microsites enriched in organic matter and nutrients. After 140 years, soil development and functionality are proved by higher TOC contents in BareS, as a result of organic matter translocation and mixing processes, which led to even higher concentrations than those in SaxS after 65 years. Microbial and fungal processes could have contributed to this TOC and N enrichment as well. Nitrogen content increased significantly in BareS with time, as

observed also in soil pit horizons. Nonetheless, unlike processes involving organic matter, TN resulted in very low concentrations even in the oldest stages, representing the major limiting factor for more nutrient-demanding plant species. Where measurable, the TOC:TN ratio was between 8 and 17.5, thus in the normal range for high-altitude grassland and tundra soils (e.g. D'Amico et al., 2014, 2015). The increase in both microbial C and N associated to the target species (and more generally to vascular species cover) along the chronosequence proved again the strong biotic impact in nutrient accumulation compared to abiotic processes, such as atmospheric deposition. In particular, the enhanced microbial biomass and activity associated to the increased concentration of C and N under the target species may have exerted a positive impact on enzyme activity and therefore on microbial N fixation. Similarly, available P content in BareS was very low, but both target species enhanced its concentration along the chronosequence confirming the priming effect of vegetation on P biocycling.

In the youngest stages (ca. 5-10 years since deglaciation) the observed accumulation of P in *Saxifraga* tissues was probably a consequence of N limitation: under drastic limiting conditions the accumulation of nutrients in tissues has been demonstrated as a possible plant physiological response (Simon et al., 2017). This may be further confirmed by the quite high C:N ratio in the herbaceous tissues, especially for *Silene* (Hobbie et al., 1998). In older stages, where organic matter and N became more abundant, P content in *Saxifraga* tissues fell to more typical values (Richardson et al., 2004). However, N:P in plant tissues was very low, along the whole chronosequence, and far from the value of 12, a threshold beyond which plant development is P-limited, such as in highly developed soils (Wardle, 2004) or in particular P-limited systems. For instance, in the Damma proglacial chronosequence (N:P ratios in the aboveground vegetation > 19, Göransson et al., 2016) the main P-containing mineral was the slowly weathering fluoroapatite (Bernasconi et al., 2011), while the Verra Grande forefield (D'Amico et al., 2020b) developed on serpentinite and almost devoid of P-bearing minerals.

Conclusion

This work provided novel results on individual plant species trajectories and related soil development through successional stages of a proglacial chronosequence. Despite the extreme conditions for plant establishment, the Lauson proglacial foreland allowed a remarkable early (5-10 years) and species-rich colonization, attained by pioneer

species in the available safe micro-sites. Carbon seemed to be the major constraint to microbial development together with N, which also hampered plant colonization. However, nutrient requirements for pioneer plants were met, likely thanks to the water fluxes funnelled between rocks. The alpine grassland species colonization started indeed immediately, although species number and cover pronouncedly increased only when the soil reached sufficient nutrient supply and functionality. Then, after about one century of ecosystem development since deglaciation, soil conditions appear suitable for the establishment of more competitive vegetation, typical of alpine grassland communities. Nonetheless, the improving effect on soil triggered by *Saxifraga oppositifolia* was already evident on quasi-inert substrates, free from ice for a limited time, highlighting the relevant role of biotic factors in stimulating the initial phases of soil formation. However, more biomass-productive species, such as *Silene acaulis*, performed a greater soil conditioning than *Saxifraga*, even within the early stage time points where both plants were present, becoming progressively more expressed with time. Therefore, C:N:P stoichiometry in proglacial areas is plant-influenced, and the impact on nutrient dynamics is related to the different species pool, with a major role played by late-successional grassland species.

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3. Relationships between vegetation, environmental factors and soil carbon stocks in alpine summer pastures

Extended paper title: Relative importance of plant species composition and environmental factors in affecting soil carbon stocks of alpine pastures (NW Italy)

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Abstract

Alpine pastures are agricultural systems with a high provision of ecosystem services, which include carbon (C) stocking. Particularly, the soil organic C (SOC) stocks of Alpine pastures may play a pivotal role in counteracting global climate change. Even if the importance of pasture SOC has been stated by several research studies, especially by comparing different land uses, little is known about the role of plant species composition. We studied a wide sample of 324 pastures in the north-western Italian Alps by performing coupled vegetation and soil surveys. Climatic (i.e., mean annual precipitation), topographic (i.e., elevation, slope, southness), vegetation (i.e., the first three dimensions of a non-metric multidimensional scaling—NMDS), and soil (i.e., pH) parameters were considered as independent variables in a generalised linear model accounting for SOC stocks in the 0–30 cm depth. Pasture SOC was significantly affected by precipitation (positively) and by pH (negatively) but not by topography. However, the higher influence was exerted by vegetation through the first NMDS dimension, which depicted a change in plant species along a thermic-altitudinal gradient. Our research highlighted the remarkable importance of vegetation in regulating SOC stocks in Alpine pastures, confirming the pivotal role of these semi-natural agricultural systems in the global scenario of climate change.

Keywords: grassland, elevation, forage, mountain, pH, precipitation, slope, vegetation

Introduction

Mountain pastures can provide many ecosystem services, such as provisioning services (e.g., biodiversity, forage), regulation and maintenance services (e.g., water purification, soil retention), and cultural services (e.g., nature-based recreation, eco-tourism) (Lavorel S. et al., 2017; Haines-Young and Potschin-Young, 2018). Among regulation services, carbon (C) stocking is of particular relevance (Canedoli et al., 2020). Carbon stocking is a key process, able to reduce the amount of atmospheric CO₂ originated by anthropogenic emissions (Lefèvre et al., 2017). Therefore, the role of land uses efficient in C stocking, namely, able to counteract current climate change, is becoming essential worldwide. Indeed, the land sinks represent the main reduction factor in the global C balance by removing about one fourth of the total emitted C (Friedlingstein et al., 2020). Part of the C is stocked in the above ground biomass (especially in woodlands), but a major portion is allocated in the soil (Lal et al., 2015). Soil organic carbon (SOC) mainly derives from the stocking of atmospheric CO₂ fixed by plants through photosynthesis and its amount can vary depending on site conditions, biotic factors, including vegetation composition, and anthropic management (Wiesmeier et al., 2019).

Although the importance of SOC stocking in slowing global warming has been widely studied (Batjes, 1996; Lefèvre et al., 2017), little is known about the role of Alpine pastures and the variability of SOC stocks related to climatic, environmental, and vegetation features e.g., Zhao et al. (2021). Specifically, several research studies compared different land uses (e.g., grasslands, forests, arable crops) in terms of their ability to stock C in the European Alps, but the importance of botanical composition within pastures has not been explored yet. It is worth mentioning that Alpine pastures in Europe are composed by a huge variety of plant species and habitats, determined by different topographic (elevation, slope, aspect), abiotic (climate, bedrock type), and biotic (pastoral management, first of all, which directly affects soil fertility) conditions (Theurillat et al., 1995; Körner, 2003).

The present study aimed at evaluating the relative importance of various abiotic and biotic (i.e., vegetation) drivers in affecting SOC stocks in a wide sample of pastures in the western Italian Alps.

Materials and Methods

The study was conducted in a wide number of Alpine valleys within the Piedmont region, north-western Italy (Figure 3.1), characterised by contrasting climatic, topographic, vegetation, and soil conditions. Between years 2000 and 2007, we surveyed 324 grassland sites, encompassing a wide geographical and ecological range. The survey sites were ascribable to 54 different vegetation types (*sensu* Cavallero et al. 2007; see Annex 3.A). All the grasslands were grazed by cattle during summers, generally with lenient stocking rates.

Elevation, slope, and southness of the sites were computed using a digital terrain model at 5-m resolution (Regione Piemonte, 2021). Mean annual precipitation was assessed at each site using a 1-km resolution raster obtained by interpolating the long-time data series (1977–2007) of 386 weather stations spread all over the region (ARPA Piemonte, 2021). Spatial analyses were carried out with QGIS v.3.16 LTR software (QGIS, 2019).

At each site, the composition of grassland vegetation was determined with the vegetation point-quadrat method (Daget and Poissonet, 1971) along 25-m transects and at 50-cm intervals. To account for species richness more accurately, the list of all occasional species not recorded along the transect but occurring in a 1-m buffer area around was completed as well (Pittarello et al., 2019; Ravetto Enri et al., 2020). Nomenclature followed Landolt et al. (2010). Then, the relative abundance of every species was calculated as the proportion in percentage of the frequency of occurrence of each species on the sum of the frequencies of all the species in each transect. A value of 0.3% was attributed to all occasional species (Ravetto Enri et al., 2020). Species relative abundances were used to perform a non-metric multidimensional scaling (NMDS) to take the vegetation composition of each survey into account in further analyses. The number of dimensions of the NMDS was defined after checking the goodness of stress value, while Bray–Curtis was specified as dissimilarity index and 100 maximum random starts were set. Species relative abundances were also used to compute some plant community variables, namely: Landolt's indicator values for temperature (T), humus (H), soil moisture (F), and soil nutrients (N) (Landolt et al., 2010), the pastoral value (PV, which is a proxy for forage productivity and quality, Daget and Poissonet, 1971), and Shannon diversity index (Magurran, 1988). These plant community variables together with species richness, were included in the NMDS biplots as supplementary variables.

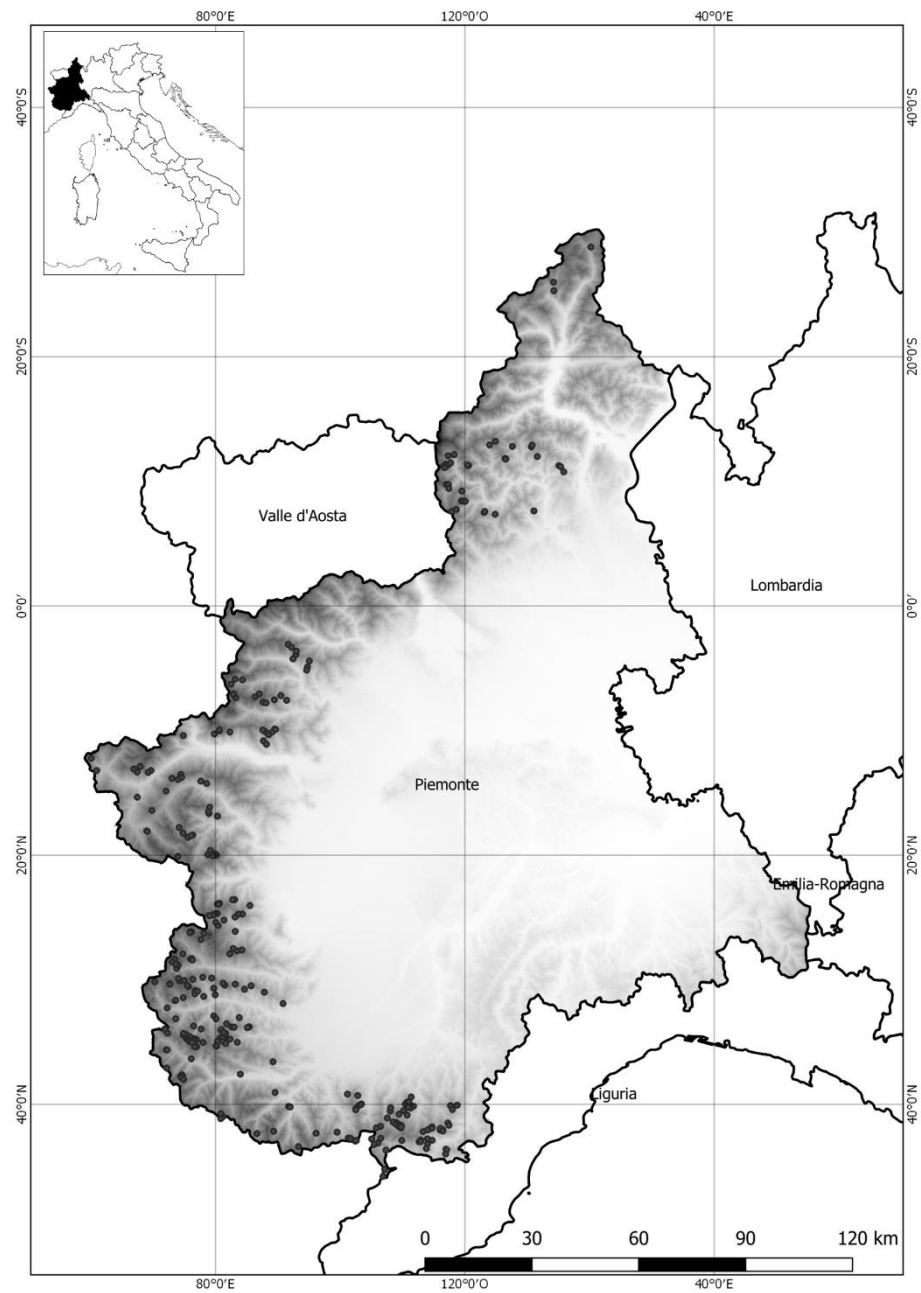


Figure 3.1. Location of the 324 survey sites in north-western Italian Alps. Each black dot represents a site.

A soil pit was dug close to each vegetation transect for soil description and sampling. The volumetric content (%) of coarse fragments, i.e., particles larger than 2 mm and smaller than 25 cm diameter, was visually assessed. Then, a soil sample of each horizon observed within the 0–30 cm depth interval was collected and transported to the laboratory. Samples were analysed for pH (soil:water = 1:2.5) according to standard soil analysis procedures (MIPAF, 1999) and an average pH value, weighted on the depth (in cm) of each observed horizon, was calculated. Organic C content was determined as well, using Walkley–Black titration (Walkley and Black, 1934).

Bulk density was estimated according to the following pedotransfer function, specifically calibrated for ‘permanent grasslands’ land use of the Alpine soil region (Calzolari et al., 2017):

$$BD = 1.565081 - 0.3946467 \times SOC - 0.0103851 \times Skel$$

where BD is the bulk density derived from the pedotransfer function and SOC and Skel are the % of OC and coarse fragments in the soil samples, respectively. Whenever Skel proportion was above 10%, the following correction was applied (Torri et al., 1994):

$$BD_c = BD \times \left[1 - 1.67 \times \left(\frac{Skel}{100} \right)^{3.39} \right]$$

where BD_c is the corrected bulk density, referred to the fine earth fraction, and Skel is the coarse fragment content by mass. The OC, BD, and Skel values were used to assess the SOC stocks at each site as the sum of SOC values of all i horizons found within the first 30 cm, weighted on their relative depth (in cm):

$$SOC_{stock} = \sum_{i=1}^n (OC_i \times BD_i \times depth_i \times (1 - Skel_i) \times 100)$$

Precipitation among the climatic variables, elevation, slope, and southness among the topographic ones, the components of the NMDS for vegetation, and soil pH were included in a generalized linear model to predict C stock. Previous to run the model, all variables were tested for autocorrelation, and standardised in order to compare the resulting β scores. Being SOC stock a continuous variable, the Gaussian and Gamma distributions were applied and the best fitting one, i.e., that one showing the lowest Akaike Information Criterion (Zuur et al., 2009), was retained. Statistical analyses were carried out in R environment, version 3.5.2 (R Core Team, 2019), using ‘goeveg’ (Goral and Schellenberg,

2021), ‘vegan’ (Oksanen et al., 2020), and ‘glmmTMB’ (Magnusson et al., 2021) packages.

Results and Discussion

Climate, Topography, and Vegetation Features

Mean annual precipitation of the studied sites ranged from 727 to 1574 mm, thus including dry to wet climatic conditions. The altitude, slope, and aspect ranged, respectively, between 988 and 2688 m a.s.l., between 0.4 and 49.8°, and between 1.1 and 179.7°. Such a wide range of topographic conditions, combined with different soils and varying effects of livestock grazing, determined a huge variability of ecological conditions and consequently a considerably high species richness. Indeed, we recorded more than 685 plant species in total and about 35 species per transect. The descriptive statistics of climatic, topographic, and vegetation features of the sites are reported in Table 3.1.

Being 0.16 the stress value of the first three dimensions of the NMDS, i.e., less than 0.20, the fitting was considered satisfactory (Clarke and Warwick, 1994). The supplementary variables included in the NMDS biplot improved the understanding of such a complex and variable vegetation, by highlighting its ecological trends in terms of plant community indices (Figure 3.2). Plant species were arranged on the first NMDS dimension according to a thermic-altitudinal gradient (Figure 3.2a), with thermophilic low-altitude species on the left side (such as *Bromus erectus* Huds., *Brachypodium rupestre* (Host) Roem. & Schult., *Lathyrus pratensis* L., *Plantago media* L., and *Rosa canina* aggr.) and those typical of cold, high-altitude environments on the right side (such as *Alchemilla pentaphyllea* L., *Carex curvula* All., *Leucanthemopsis alpina* (L.) Heywood, *Phyteuma globularifolium* Sternb. & Hoppe, and *Salix herbacea* L.). The arrow of Landolt’s T confirmed this gradient, being left-directed and close to the horizontal axis. The second dimension was related to the storage of dead organic material (as outlined by Landolt’s H arrow), with species growing on soils poor in humus in the upper part of the graph (such as *Anthyllis vulneraria* L., *Helianthemum oelandicum* (L.) Dum. Cours., *Helictotrichon sedenense* (DC.) Holub, *Onobrychis montana* DC., and *Sesleria caerulea* (L.) Ard.) and species found on soils with higher humus content at the bottom (such as *Calluna vulgaris* (L.) Hull, *Potentilla erecta* (L.) Raeusch., *Carex pallescens* L., *Agrostis capillaris* L., *Poa chaixii* Vill.). Finally, the distribution of the species on the third dimension showed a positive

gradient of soil nutrient and forage quality, as shown by the position of Landolt's N and PV arrows, respectively. Indeed, in Figure 3.2b the species typical of nutrient rich environments, such as *Taraxacum officinale* s.l., *Peucedanum ostruthium* (L.) W.D.J. Koch, *Poa pratensis* L., *Geranium sylvaticum* L., and *Silene vulgaris* (Moench) Garcke, were in the upper part of the biplot, while those typical of nutrient-poor pastures, such as *Festuca paniculata* (L.) Schinz & Thell., *C. vulgaris*, *Vaccinium myrtillus* L., *Chamaecytisus hirsutus* (L.) Link, and *Gymnadenia conopsea* (L.) R. Br., were at the bottom.

Table 3.1. Climatic, topographic, and vegetation descriptors of the 324 sites. SE, standard error of the mean; Landolt's indicators: F, soil moisture; N, soil nutrients; H, humus; T, temperature.

Variable	Min	25 %	Median	75 %	Max	Mean	SE
Climate							
Precipitation [mm y ⁻¹]	726.9	900.4	962.3	1103.5	1574.1	1008.2	8.88
Topography							
Elevation [m a.s.l.]	988	1813	2094	2329	2688	2041	20.0
Slope [°]	0.4	12.9	20.8	28.8	49.8	20.9	0.57
Southness [°]	1.1	78.7	124.9	155.9	179.7	111.9	2.91
Vegetation							
Species richness	9	26	35	44	62	35	0.7
Shannon index	1.3	3.2	3.7	4.1	5.0	3.6	0.04
Landolt's F	1.6	2.3	2.6	2.9	4.2	2.6	0.02
Landolt's N	1.6	2.2	2.4	2.7	4.7	2.5	0.02
Landolt's H	1.9	3.0	3.2	3.4	4.9	3.2	0.02
Landolt's T	1.9	1.9	2.3	2.7	3.9	2.3	0.03
Pastoral Value	20.9	34.4	40.6	46.3	73.1	41.2	0.51

3. Relationships between vegetation, environmental factors and soil carbon stocks in alpine summer pastures

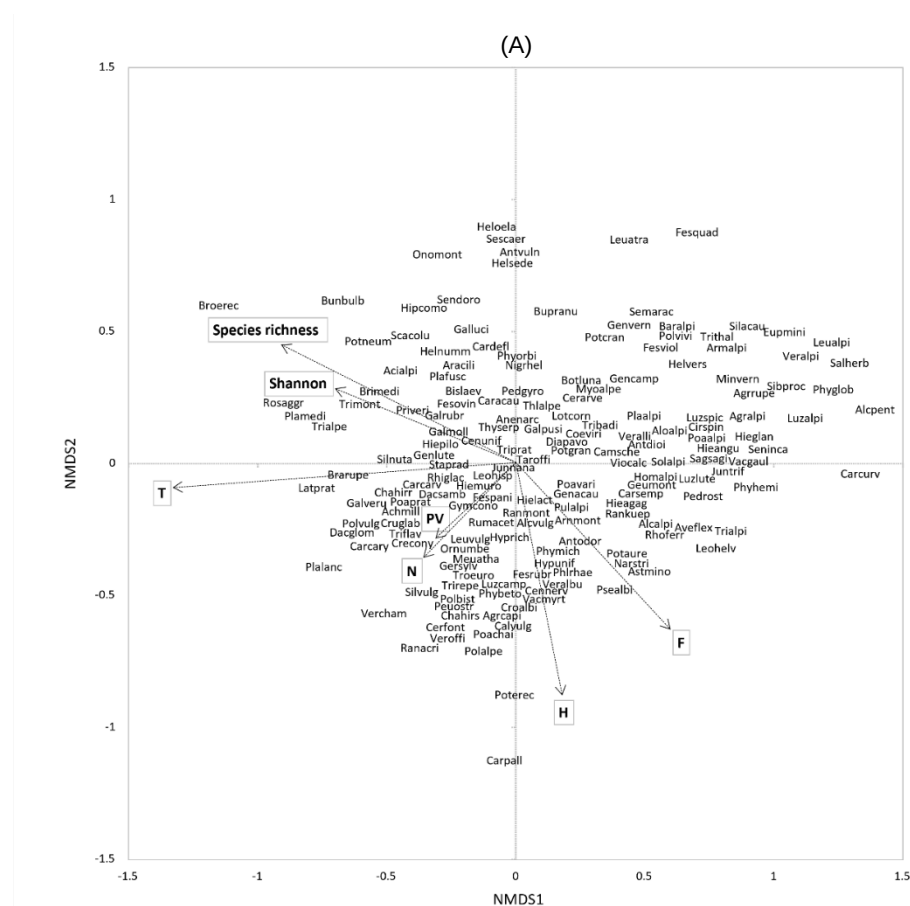


Figure 3.2. Cont.

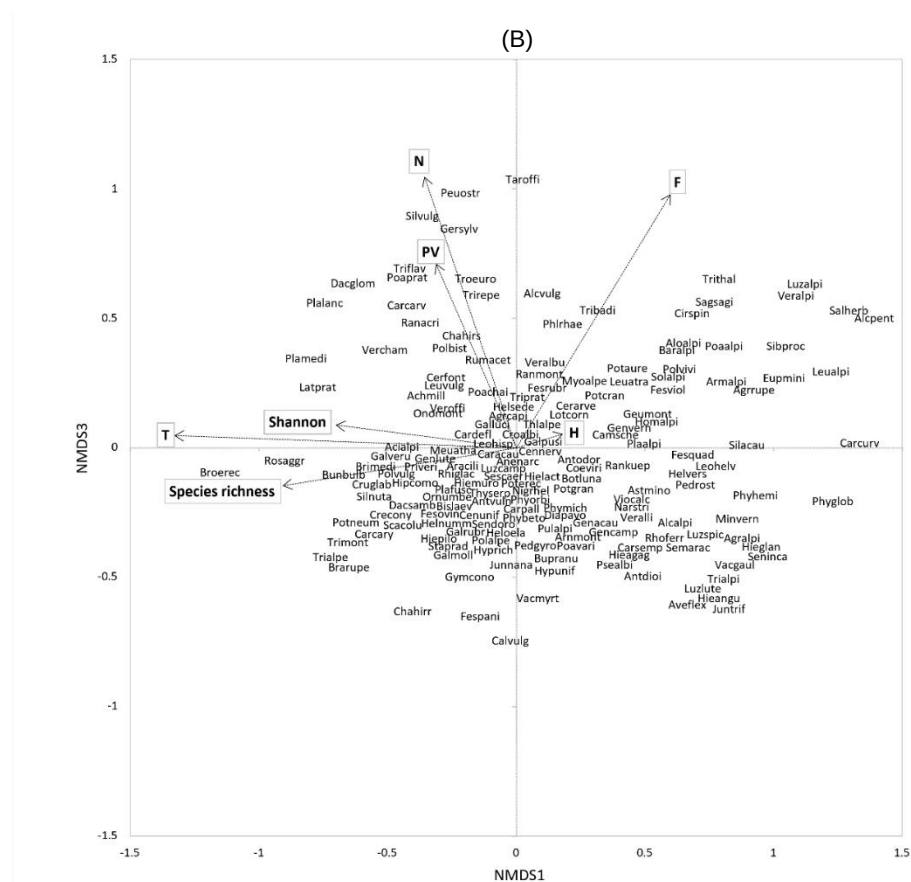


Figure 3.2. Biplots of the non-metric multidimensional scaling (NMDS): (A) first and second dimensions, (B) first and third dimensions. Stress value for the three dimensions: 0.16. Only species recorded in more than 5% of the surveys are displayed and identified by a species code (see Annex 3.B for the complete species and code list). Dashed arrows represent passive variables: biodiversity (species richness and Shannon diversity index), Landolt's indicator values (F, soil moisture; H, humus; N, soil nutrients; T, temperature), and pastoral value (PV).

Soil Features

The soil pH encompassed both acidic and basic soil conditions, ranging from 3.3 to 8.3 (Table 3.2). Soil C stock in the investigated pastures ranged between 1.9 and 234.9 t ha⁻¹, with an average value of 87.8 t ha⁻¹. Such values were higher when compared to those of other land uses (arable lands: 52.6 ± 5.56; permanent crops: 41.4 ± 2.06; woodlands: 71.4 ± 2.10; t ha⁻¹ ± standard error), which were recorded with the same methods in the same region during a previous trial (Calzolari et al., 2017). Rodríguez-Murillo (2001) and Hoffmann et al. (2014) found similar SOC contents in Spanish and Swiss pastures, respectively. Another recent study conducted by Ferré et al. (2020) on Italian alpine grasslands reported lower values of C stocks. However, this trial was carried out in a single 1.5-ha study area characterised by a limited variability of ecological conditions, and the related outcomes should be considered with caution consequently. Canedoli et al. (2020) in north-western Italy and Liefeld et al. (2005) in Switzerland reported lower C stocks compared to our trial, but at the same time they highlighted higher SOC values in grasslands than in the woodlands and the arable lands, respectively, highlighting a similar trend. This may be due to the accumulation of OC in the upper soil horizons, which is particularly relevant in well-managed alpine pastures if compared to forests (Guidi et al., 2014). Indeed, the positive role of Alpine grasslands as CO₂ sinks may be exerted only with an active and balanced pastoral management, thus avoiding both overgrazing and abandonment (Meyer et al., 2012; Garcia-Pausas et al., 2017). Other research studies located in the European Alps reported SOC amounts characterised by wide variability, but they did not consider the role of differing plant species composition in determining the variations of soil bio-chemical features (Kopáček et al., 2006; Djukic et al., 2010).

Table 3.2. Soil descriptors of the 324 sites. SE, standard error of the mean.

Variable	Min	25 %	Median	75 %	Max	Mean	SE
pH	3.3	4.6	5.0	5.8	8.3	5.3	0.06
Coarse fragment content [%]	0.0	6.8	15.9	25.8	70.0	18.5	0.81
Bulk density [t m ⁻³]	0.2	0.7	0.9	1.0	1.2	0.8	0.01
Soil organic carbon [t ha ⁻¹]	1.9	59.2	87.8	112.8	234.9	87.8	2.09

Modelling Soil Organic Carbon Stocks

Data analysed through generalised linear model with Gaussian distribution showed a lower Akaike information criterion when compared to Gamma one (3237 vs. 3287) thus the relative model results were retained. Model outputs highlighted the relative importance of each factor in affecting SOC stocks (Table 3.3), providing new knowledge through a comprehensive approach concerning the role of vegetation in C bio-cycling of European Alpine pastures, which was scanty focused till present. Among the selected variables, those exerting a significant influence on SOC stocks were precipitation, vegetation (particularly, the first dimension of the NMDS), and soil pH. Conversely, elevation, slope, and southness showed non-significant effects as well as the second and third NMDS dimensions. The limited importance of southness and slope confirmed the outcomes of a previous trial (Garcia-Pausas et al., 2007), which, however, reported significant negative effects of both elevation and precipitation. In the present study, the precipitation showed a positive influence on SOC, likely due to an indirect effect on biomass production, which is generally associated to higher C stocks (Yang et al., 2010).

However, vegetation was found to be the most important driver, as highlighted by the highest β score. Its negative sign showed that higher SOC stocks were recorded in pastures with higher proportions of those species distributed on the left side of Figure 3.2a, i.e., in pastures rich in plants typical of warm, low-altitude, species-rich environments. Similar to precipitation, species typical of warmer pastures (proxied by Landolt's T value) may be associated to greater biomass production, with positive effects on SOC content (Yang et al., 2010). Species richness may exert a positive influence on C stocking as well, since it generally corresponds to a diversity of root systems (characterised by differing depths, biomasses, C storages, etc.) and to an enhanced soil microbial diversity (which improves SOC transformation and degradation), which indirectly influences decomposition processes (Steinbeiss et al., 2008; Tian et al., 2016). Surprisingly, a significant effect of the second dimension of NMDS (i.e., a vegetational proxy of soil humus content) on SOC was not observed. This may depend on humus type, which could affect SOC content but is not taken into account by Landolt's H (Landolt et al., 2010; Kukuls et al., 2020). However, further investigations are needed to clarify this relationship. Finally, the lack of a significant effect of the third dimension of NMDS (related to soil fertility) was likely expected. Indeed, in this study, the pastures with low Landolt's N and PV, i.e., with low soil fertility due to undergrazing (Pittarello et al., 2018), were encroached by

shrubs, such as *C. vulgaris*, *V. myrtillus*, and *C. hirsutus*. Likely, the low biochemical quality of shrub litter delayed its decomposition and allowed higher organic matter accumulations in the topsoil (Garcia-Pausas et al., 2017). However, the effect of shrub proliferation at a depth greater than the 30 cm considered here was partially unclear since the low root turnover of shrubs compared to grasses should have reduced the C inputs in the soil.

As for pH, larger amounts of SOC were recorded in soils with an acidic reaction, confirming the remarkable importance of pH in affecting SOC stocks in Alpine grasslands (Liao et al., 2016), probably because low pH is associated to high SOC contents, or mineralisation is reduced at low pH (Curtin et al., 1998; Sapek, 1996).

Table 3.3. Results of the generalized linear model accounting for the stock of soil organic carbon. NMDS, non-metric multidimensional scaling; SE, standard error; ***, $p < 0.001$; **, $p < 0.01$.

	β Score	SE	p Value	Sig.
(Intercept)	87.787	1.928	<0.001	***
Precipitation	9.994	2.515	<0.001	***
Elevation	7.619	4.206	0.070	
Slope	0.241	2.325	0.917	
Southness	0.182	2.237	0.935	
NMDS1	-11.782	4.068	0.004	**
NMDS2	-3.611	2.897	0.213	
NMDS3	-1.991	2.219	0.370	
pH	-8.574	2.752	0.002	**

According to our results, the SOC stocking of Alpine pastures, generally managed under extensive grazing regimes, was predominantly influenced by the vegetation rather than by abiotic factors. More specifically, we observed a remarkable role of warm-pasture species (such as *B. erectus*), which might have a limited interest as fodder resource (in terms of quantity and quality, Pornaro et al., 2019), but which can definitely have a remarkable weight on carbon stocks. Dry pastures, which generally host large proportions of such plants, are widely represented in the Alps. For instance, the dry grasslands

dominated by *B. rupestre*, *F. paniculata*, or *F. ovina* aggr. cover more than 30% of the pasture area in Piedmont Region (Cavallero et al., 2007). The importance of alpine pastures in SOC stocking was in general confirmed, as the observed values were generally higher compared to other land uses. Thus, pasture conservation policies should be encouraged, such as through specific PES (payments for ecosystem services) (Rodríguez-Ortega et al., 2018). In the current scenario of climate change, the abundance of warm grassland species will likely increase in the future years (Theurillat and Guisan, 2001), and a shift at higher elevations would be expected. Consequently, an increase of SOC stocks in Alpine pastures might be observed but, precipitation being a relevant factor affecting C cycling as well, a targeted monitoring should be carried out to take the complex and spatially heterogeneous patterns of climate change into account (Sun et al., 2017; Masson-Delmotte et al., 2021).

Future research should be addressed to monitor the possible effects of management intensity, for instance of different stocking rates or grazing regimes. Moreover, the SOC stocking ability of permanent pasture should be compared with that of mountain hay meadows. An extension would be advisable to lowland grasslands too, where the species richness and diversity are generally lower compared to the mountain ones, and which are generally more intensively managed in terms of number of exploitations per year and fertilisation.

Conclusions

The novel results of this study carried out in a huge range of ecological conditions highlighted the relevant importance of grassland species composition in affecting soil C stock of Alpine soils, while topographic attributes had negligible effects. More specifically, dry pastures (which also generally host rare plants and a high species richness) stocked more carbon in the upper soil horizons. Among abiotic factors, precipitation positively affected soil organic carbon stocks, likely through an indirect effect due to the increased herbage biomass. Thus, higher SOC values were found on acidic soils, where mineralization might be hampered. Future conservation strategies should aim to consider the role of such extensively managed pastures, which can be found in the Alpine region, and of the dry grassland species in enhancing this ecosystem service.

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Annex 3.A

List of vegetation types (*sensu* Cavallero et al. 2007) surveyed in the 324 pastures. The dominant plant species and the number of surveys performed per each vegetation type is provided. Scientific binomials followed Landolt et al. (2010).

Vegetation type	Surveys
<i>Agrostis schraderana</i>	2
<i>Alchemilla</i> gr. <i>alpina</i>	1
<i>Alchemilla</i> gr. <i>vulgaris</i>	5
<i>Alchemilla pentaphyllea</i>	5
<i>Alopecurus gerardi</i>	2
<i>Brachypodium caespitosum</i> / <i>rupestre</i>	18
<i>Briza media</i>	1
<i>Bromus erectus</i>	11
<i>Calamagrostis villosa</i>	1
<i>Carex curvula</i>	4
<i>Carex fimbriata</i>	2
<i>Carex foetida</i>	3
<i>Carex fusca</i>	2
<i>Carex humilis</i>	2
<i>Carex rupestris</i>	2
<i>Carex sempervirens</i>	5
<i>Carex tendae</i>	1
<i>Dactylis glomerata</i>	10
<i>Dryas octopetala</i>	1
<i>Elyna myosuroides</i>	1
<i>Festuca</i> gr. <i>halleri</i>	1
<i>Festuca</i> gr. <i>ovina</i>	18
<i>Festuca</i> gr. <i>rubra</i> and <i>Agrostis tenuis</i>	41
<i>Festuca</i> gr. <i>violacea</i>	14
<i>Festuca paniculata</i>	21
<i>Festuca scabriculum</i>	5
<i>Hedysarum brigantiacum</i>	2
<i>Helianthemum nummularium</i>	3
<i>Helianthemum oelandicum</i>	1
<i>Helictotrichon parlatorei</i>	5
<i>Ligusticum mutellina</i>	2
<i>Luzula alpino-pilosa</i>	1
<i>Molinia arundinacea</i>	1
<i>Molinia coerulea</i>	1

Vegetation type	Surveys
<i>Nardus stricta</i>	53
<i>Onobrychis montana</i>	10
<i>Petasites hybridus</i>	1
<i>Phleum alpinum</i>	1
<i>Plantago alpina</i>	1
<i>Poa alpina</i>	2
<i>Poa violacea</i>	7
<i>Polygonum bistorta</i>	2
<i>Polygonum viviparum</i>	3
<i>Rumex alpinus</i>	1
<i>Salix herbacea</i>	2
<i>Scirpus sylvaticus</i>	1
<i>Sesleria varia</i>	7
<i>Stipa pennata</i>	2
<i>Taraxacum officinale</i>	1
<i>Trifolium alpinum</i> and <i>Carex sempervirens</i>	26
<i>Trifolium thalii</i>	2
<i>Trisetum flavescens</i>	4
<i>Vaccinium gaultherioides</i>	2
<i>Vaccinium myrtillus</i>	1
Total	324

Cavallero A., Aceto P., Gorlier A., Lombardi G., Lonati M., Martinasso B., and Tagliatori C., 2007. *I tipi pastorali delle Alpi piemontesi: vegetazione e gestione dei pascoli delle Alpi occidentali*; Alberto Perdisa Editore: Bologna, Italy, 2007; ISBN 978-88-8372-321-6.

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Annex 3.B

List of plant species recorded in the 324 vegetation transects. The species code displayed in the biplots of the non-metric multidimensional scaling (NMDS), the number and proportion of transects where the species was found, and the average species relative abundance (SRA) are reported. Scientific binomials followed Landolt et al. (2010).

Species name	Species code	Transects		SRA
		n	%	
<i>Abies alba</i>		1	0%	0.30
<i>Acer pseudoplatanus</i>		2	1%	0.50
<i>Achillea erba-rotta</i>		2	1%	0.30
<i>Achillea macrophylla</i>		1	0%	2.84
<i>Achillea millefolium</i> aggr.	Achmill	133	41%	0.30
<i>Achillea moschata</i>		1	0%	2.29
<i>Achillea nana</i>		3	1%	0.66
<i>Achnatherum calamagrostis</i>		2	1%	0.63
<i>Acinos alpinus</i>	Acialpi	26	8%	0.30
<i>Aconitum napellus</i>		3	1%	2.29
<i>Adenostyles leucophylla</i>		1	0%	4.04
<i>Aegopodium podagraria</i>		4	1%	4.03
<i>Agrostis alpina</i>	Agralpi	52	16%	4.05
<i>Agrostis canina</i>		1	0%	6.29
<i>Agrostis capillaris</i>	Agrcapi	125	39%	2.25
<i>Agrostis rupestris</i>	Agrrupe	33	10%	8.63
<i>Agrostis schraderiana</i>		16	5%	0.44
<i>Ajuga genevensis</i>		5	2%	0.37
<i>Ajuga pyramidalis</i>		10	3%	0.84
<i>Ajuga reptans</i>		8	2%	2.12
<i>Alchemilla alpina</i> aggr.	Alcalpi	59	18%	8.66
<i>Alchemilla pentaphyllea</i>	Alcpent	26	8%	2.91
<i>Alchemilla vulgaris</i> aggr.	Alcvulg	126	39%	0.30
<i>Allium carinatum</i>		1	0%	0.45
<i>Allium lusitanicum</i>		2	1%	7.06
<i>Allium narcissiflorum</i>		2	1%	0.30
<i>Allium oleraceum</i>		2	1%	0.77
<i>Allium schoenoprasum</i>		8	2%	0.40
<i>Allium sphaerocephalon</i>		6	2%	0.30
<i>Alnus viridis</i>		9	3%	4.12
<i>Alopecurus alpinus</i>	Aloalpi	50	15%	0.30
<i>Alyssum alyssoides</i>		2	1%	0.47
<i>Alyssum montanum</i>		4	1%	0.30
<i>Anacamptis pyramidalis</i>		1	0%	0.65
<i>Androsace obtusifolia</i>		10	3%	1.88
<i>Androsace vitaliana</i>		8	2%	1.88
<i>Androsace adfinis</i>		3	1%	0.42

Species name	Species code	Transects		SRA
		n	%	
<i>Anemone baldensis</i>		5	2%	1.53
<i>Anemone narcissiflora</i>	Anenarc	28	9%	1.54
<i>Anemone nemorosa</i>		6	2%	1.06
<i>Anemone ranunculoides</i>		1	0%	0.30
<i>Angelica sylvestris</i>		1	0%	0.64
<i>Antennaria carpatica</i>		8	2%	0.63
<i>Antennaria dioica</i>	Antdioi	61	19%	1.86
<i>Anthericum liliago</i>		9	3%	3.05
<i>Anthoxanthum odoratum</i> aggr.	Antodor	180	56%	5.54
<i>Anthriscus sylvestris</i>		2	1%	4.00
<i>Anthyllis montana</i>		2	1%	1.53
<i>Anthyllis vulneraria</i>	Antvuln	41	13%	0.30
<i>Aphanes arvensis</i>		1	0%	0.30
<i>Arabidopsis thaliana</i>		1	0%	0.38
<i>Arabis allionii</i>		5	2%	0.30
<i>Arabis auriculata</i>		1	0%	0.31
<i>Arabis ciliata</i>	Aracili	21	6%	0.55
<i>Arabis hirsuta</i>		8	2%	0.30
<i>Arctium minus</i>		1	0%	3.67
<i>Arctium nemorosum</i>		1	0%	0.30
<i>Arenaria biflora</i>		1	0%	0.43
<i>Arenaria ciliata</i>		14	4%	1.03
<i>Arenaria serpyllifolia</i> aggr.		7	2%	0.31
<i>Armeria alpina</i>	Armalpi	33	10%	2.60
<i>Armeria arenaria</i>		8	2%	0.88
<i>Arnica montana</i>	Arnmont	88	27%	1.63
<i>Arrhenatherum elatius</i>		7	2%	0.54
<i>Artemisia absinthium</i>		5	2%	6.40
<i>Artemisia campestris</i>		2	1%	0.30
<i>Artemisia glacialis</i>		2	1%	0.91
<i>Asperula cynanchica</i>		6	2%	0.30
<i>Asperula purpurea</i>		1	0%	2.24
<i>Asphodelus macrocarpus</i>		13	4%	0.76
<i>Aster alpinus</i>		15	5%	1.73
<i>Aster bellidiastrum</i>		12	4%	2.36
<i>Astragalus alpinus</i>		8	2%	0.30
<i>Astragalus australis</i>		1	0%	5.56
<i>Astragalus cicer</i>		1	0%	3.93
<i>Astragalus danicus</i>		6	2%	0.30
<i>Astragalus glycyphyllos</i>		2	1%	0.67
<i>Astragalus monspessulanus</i>		11	3%	0.30
<i>Astragalus penduliflorus</i>		3	1%	0.93
<i>Astragalus sempervirens</i>		4	1%	0.65
<i>Astrantia major</i>		5	2%	0.86
<i>Astrantia minor</i>	Astmino	21	6%	0.30

3. Relationships between vegetation, environmental factors and soil carbon stocks
in alpine summer pastures

Species name	Species code	Transects		SRA
		n	%	
<i>Athamanta cretensis</i>		1	0%	0.30
<i>Athyrium filix-femina</i>		2	1%	5.02
<i>Avenella flexuosa</i>	Aveflex	109	34%	0.30
<i>Barbarea intermedia</i>		4	1%	0.68
<i>Bartsia alpina</i>	Baralpi	23	7%	0.30
<i>Bellis perennis</i>		2	1%	0.30
<i>Berberis vulgaris</i>		2	1%	0.30
<i>Betula pendula</i>		4	1%	0.45
<i>Biscutella laevigata</i>	Bislaev	75	23%	0.42
<i>Botrychium lunaria</i>	Botluna	30	9%	14.56
<i>Brachypodium rupestre</i>	Brarupe	55	17%	2.10
<i>Briza media</i>	Brimedi	35	11%	16.75
<i>Bromus erectus</i>	Broerrec	20	6%	0.30
<i>Bromus inermis</i>		1	0%	0.30
<i>Buglossoides arvensis</i>		1	0%	0.70
<i>Bunium bulbocastanum</i>	Bunbulb	20	6%	0.30
<i>Bupthalmum salicifolium</i>		1	0%	0.30
<i>Bupleurum falcatum</i>		2	1%	1.80
<i>Bupleurum ranunculoides</i>	Bupranu	25	8%	1.30
<i>Calamagrostis arundinacea</i>		2	1%	0.30
<i>Calamagrostis varia</i>		1	0%	26.21
<i>Calamagrostis villosa</i>		1	0%	10.26
<i>Callianthemum coriandrifolium</i>		1	0%	3.82
<i>Calluna vulgaris</i>	Calvulg	34	10%	0.69
<i>Campanula barbata</i>		16	5%	0.30
<i>Campanula cochleariifolia</i>		1	0%	0.88
<i>Campanula excisa</i>		1	0%	0.68
<i>Campanula glomerata</i>		6	2%	0.61
<i>Campanula persicifolia</i>		5	2%	0.96
<i>Campanula rhomboidalis</i>		1	0%	0.87
<i>Campanula scheuchzeri</i>	Camsche	167	52%	0.58
<i>Capsella bursa-pastoris</i>		6	2%	0.30
<i>Cardamine alpina</i>		1	0%	0.68
<i>Cardamine resedifolia</i>		10	3%	3.47
<i>Cardaminopsis halleri</i>		3	1%	1.02
<i>Carduus defloratus</i>	Cardefl	82	25%	14.18
<i>Carex acuta</i>		1	0%	0.99
<i>Carex aterrima</i>		5	2%	1.14
<i>Carex atrata</i>		2	1%	4.27
<i>Carex caryophyllea</i>	Carcary	23	7%	9.78
<i>Carex curvula</i>	Carcurv	18	6%	7.62
<i>Carex echinata</i>		1	0%	1.11
<i>Carex ericetorum</i>		3	1%	20.51
<i>Carex fimbriata</i>		2	1%	4.94
<i>Carex flacca</i>		3	1%	16.27

Species name	Species code	Transects		SRA
		n	%	
<i>Carex flava</i> aggr.		3	1%	17.45
<i>Carex foetida</i>		15	5%	3.50
<i>Carex hirta</i>		1	0%	8.19
<i>Carex humilis</i>		17	5%	1.43
<i>Carex leporina</i>		11	3%	31.43
<i>Carex nigra</i>		3	1%	1.72
<i>Carex ornithopoda</i>		17	5%	2.52
<i>Carex pallescens</i>	Carpall	20	6%	4.77
<i>Carex panicea</i>		4	1%	1.90
<i>Carex paniculata</i>		1	0%	2.34
<i>Carex parviflora</i>		4	1%	1.46
<i>Carex pauciflora</i>		2	1%	5.01
<i>Carex pilulifera</i>		3	1%	1.19
<i>Carex rosae</i>		7	2%	16.43
<i>Carex rupestris</i>		4	1%	8.81
<i>Carex sempervirens</i>	Carsemp	207	64%	1.08
<i>Carex spicata</i>		1	0%	3.40
<i>Carex tendae</i>		7	2%	0.30
<i>Carlina acanthifolia</i>		1	0%	1.05
<i>Carlina acaulis</i>	Caracau	70	22%	0.63
<i>Carlina vulgaris</i>		2	1%	1.68
<i>Carum carvi</i>	Carcarv	30	9%	0.30
<i>Castanea sativa</i>		1	0%	0.76
<i>Centaurea nervosa</i>	Cennerv	18	6%	0.66
<i>Centaurea nigra</i>		11	3%	0.90
<i>Centaurea scabiosa</i>		15	5%	1.38
<i>Centaurea triumfettii</i>		16	5%	0.77
<i>Centaurea uniflora</i>	Cenunif	64	20%	0.30
<i>Cephalanthera longifolia</i>		2	1%	0.98
<i>Cerastium arvense</i>	Cerarve	123	38%	1.91
<i>Cerastium cerastoides</i>		2	1%	0.79
<i>Cerastium fontanum</i>	Cerfont	27	8%	0.73
<i>Cerinthe glabra</i>		3	1%	0.30
<i>Cerinthe minor</i>		2	1%	2.26
<i>Chaerophyllum hirsutum</i>	Chahirs	29	9%	3.31
<i>Chamaecytisus hirsutus</i>	Chahirr	31	10%	0.75
<i>Chenopodium bonus-henricus</i>		15	5%	0.62
<i>Cirsium acaule</i>		6	2%	0.30
<i>Cirsium arvense</i>		1	0%	0.50
<i>Cirsium eriophorum</i>		5	2%	0.91
<i>Cirsium palustre</i>		3	1%	0.42
<i>Cirsium spinosissimum</i>	Cirspin	26	8%	0.40
<i>Cirsium vulgare</i>		8	2%	1.05
<i>Clinopodium vulgare</i>		10	3%	0.39
<i>Coeloglossum viride</i>	Coeviri	19	6%	0.78

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Species name	Species code	Transects		SRA
		n	%	
<i>Colchicum alpinum</i>		1	0%	0.32
<i>Colchicum autumnale</i>		11	3%	0.30
<i>Conopodium majus</i>		1	0%	0.30
<i>Corylus avellana</i>		1	0%	0.30
<i>Cotoneaster integerrimus</i>		3	1%	0.30
<i>Crataegus monogyna</i>		2	1%	0.89
<i>Crepis aurea</i>		4	1%	1.20
<i>Crepis conyzifolia</i>	Crecony	39	12%	1.57
<i>Crepis paludosa</i>		2	1%	2.39
<i>Crocus albiflorus</i>	Croalbi	64	20%	1.45
<i>Cruciata glabra</i>	Cruglab	50	15%	0.85
<i>Cruciata laevipes</i>		4	1%	0.30
<i>Crupina vulgaris</i>		1	0%	0.30
<i>Cryptogramma crispa</i>		2	1%	0.63
<i>Cuscuta epithymum</i>		1	0%	1.55
<i>Cynosurus cristatus</i>		7	2%	0.67
<i>Cytisophyllum sessilifolium</i>		2	1%	0.30
<i>Cytisus scoparius</i>		3	1%	5.75
<i>Dactylis glomerata</i>	Dacglom	50	15%	0.30
<i>Dactylorhiza maculata</i>		4	1%	0.30
<i>Dactylorhiza majalis</i>		1	0%	0.34
<i>Dactylorhiza sambucina</i>	Dacsamb	18	6%	4.32
<i>Danthonia decumbens</i>		15	5%	0.30
<i>Daphne mezereum</i>		12	4%	0.50
<i>Daucus carota</i>		2	1%	3.00
<i>Deschampsia cespitosa</i>		7	2%	1.64
<i>Dianthus carthusianorum</i>		13	4%	0.57
<i>Dianthus deltoides</i>		8	2%	1.43
<i>Dianthus furcatus</i>		12	4%	0.74
<i>Dianthus pavonius</i>	Diapavo	112	35%	0.30
<i>Dianthus superbus</i>		3	1%	1.15
<i>Dianthus sylvestris</i>		7	2%	0.30
<i>Digitalis grandiflora</i>		2	1%	0.30
<i>Doronicum grandiflorum</i>		2	1%	0.36
<i>Draba aizoides</i>		9	3%	5.86
<i>Dryas octopetala</i>		9	3%	0.30
<i>Dryopteris filix-mas</i>		5	2%	0.30
<i>Echinops ritro</i>		1	0%	0.30
<i>Echium vulgare</i>		3	1%	0.30
<i>Elymus repens</i>		1	0%	4.73
<i>Elyna myosuroides</i>		15	5%	0.30
<i>Empetrum hermaphroditum</i>		1	0%	0.30
<i>Epilobium angustifolium</i>		4	1%	2.40
<i>Epilobium fleischeri</i>		1	0%	0.76
<i>Epilobium montanum</i>		1	0%	0.30

Species name	Species code	Transects		SRA
		n	%	
<i>Epilobium palustre</i>		2	1%	3.81
<i>Equisetum arvense</i>		1	0%	0.41
<i>Erigeron alpinus</i>		11	3%	0.30
<i>Erigeron annuus</i>		1	0%	0.60
<i>Erigeron uniflorus</i>		10	3%	3.09
<i>Eriophorum angustifolium</i>		3	1%	1.71
<i>Eriophorum latifolium</i>		2	1%	5.88
<i>Eriophorum scheuchzeri</i>		1	0%	0.96
<i>Eritrichium nanum</i>		1	0%	0.30
<i>Eryngium campestre</i>		1	0%	0.92
<i>Erysimum jugicola</i>		6	2%	0.30
<i>Erysimum virgatum</i>		2	1%	0.78
<i>Euphorbia cyparissias</i>		5	2%	1.98
<i>Euphorbia dulcis</i>		3	1%	0.47
<i>Euphrasia alpina</i>		16	5%	0.30
<i>Euphrasia hirtella</i>		1	0%	0.83
<i>Euphrasia minima</i>	Eupmini	19	6%	1.03
<i>Euphrasia rostkoviana</i>		1	0%	0.83
<i>Euphrasia stricta</i>		12	4%	0.30
<i>Fagus sylvatica</i>		2	1%	2.83
<i>Festuca arundinacea</i>		2	1%	5.50
<i>Festuca dimorpha</i>		2	1%	3.34
<i>Festuca filiformis</i>		6	2%	15.64
<i>Festuca flavescens</i>		2	1%	4.60
<i>Festuca gigantea</i>		3	1%	5.93
<i>Festuca halleri</i> aggr.		13	4%	8.66
<i>Festuca ovina</i> aggr.	Fesovin	160	49%	12.36
<i>Festuca paniculata</i>	Fespani	62	19%	3.99
<i>Festuca pratensis</i>		4	1%	4.90
<i>Festuca quadriflora</i>	Fesquad	24	7%	10.26
<i>Festuca rubra</i>	Fesrubr	163	50%	11.50
<i>Festuca scabriculumis</i>		17	5%	8.90
<i>Festuca violacea</i> aggr.	Fesviol	82	25%	0.40
<i>Fourraea alpina</i>		9	3%	0.95
<i>Fragaria vesca</i>		8	2%	0.71
<i>Fraxinus excelsior</i>		3	1%	0.36
<i>Fritillaria tubaeformis</i>		4	1%	3.28
<i>Gagea fragifera</i>		2	1%	9.84
<i>Galeopsis ladanum</i>		1	0%	0.30
<i>Galeopsis pubescens</i>		1	0%	0.71
<i>Galeopsis tetrahit</i>		5	2%	16.67
<i>Galium laevigatum</i>		1	0%	1.32
<i>Galium lucidum</i> aggr.	Galluci	21	6%	1.77
<i>Galium mollugo</i> aggr.	Galmoll	22	7%	0.98
<i>Galium pusillum</i> aggr.	Galpusi	60	19%	0.98

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		n	%	
<i>Galium rubrum</i> aggr.	Galrubr	40	12%	0.90
<i>Galium verum</i>	Galveru	37	11%	5.39
<i>Genista cinerea</i>		2	1%	1.54
<i>Genista germanica</i>		17	5%	2.36
<i>Genista pilosa</i>		7	2%	1.31
<i>Genista tinctoria</i>		12	4%	0.93
<i>Gentiana acaulis</i> aggr.	Genacau	89	27%	0.34
<i>Gentiana campestris</i> aggr.	Gencamp	26	8%	0.30
<i>Gentiana cruciata</i>		1	0%	0.36
<i>Gentiana lutea</i>	Genlute	23	7%	0.77
<i>Gentiana nivalis</i>		3	1%	0.36
<i>Gentiana punctata</i> aggr.		6	2%	0.30
<i>Gentiana purpurea</i>		1	0%	0.52
<i>Gentiana ramosa</i>		3	1%	0.63
<i>Gentiana verna</i>	Genvern	53	16%	0.30
<i>Geranium molle</i>		2	1%	0.34
<i>Geranium pyrenaicum</i>		4	1%	1.67
<i>Geranium sylvaticum</i>	Gersylv	34	10%	2.43
<i>Geum montanum</i>	Geumont	128	40%	0.30
<i>Geum rivale</i>		1	0%	1.03
<i>Globularia bisnagarica</i>		8	2%	2.45
<i>Globularia cordifolia</i>		14	4%	6.24
<i>Gnaphalium hoppeanum</i>		2	1%	0.65
<i>Gnaphalium norvegicum</i>		2	1%	1.56
<i>Gnaphalium supinum</i>		17	5%	0.52
<i>Gnaphalium sylvaticum</i>		4	1%	0.41
<i>Gymnadenia conopsea</i>	Gymcono	26	8%	1.94
<i>Gymnocarpium dryopteris</i>		1	0%	0.30
<i>Gypsophila repens</i>		5	2%	10.97
<i>Hedysarum hedysaroides</i>		6	2%	0.30
<i>Helianthemum apenninum</i>		2	1%	4.69
<i>Helianthemum nummularium</i>	Helnumm	85	26%	3.05
<i>Helianthemum oelandicum</i> aggr.	Heloela	32	10%	14.45
<i>Helictotrichon parlatorei</i>		16	5%	3.59
<i>Helictotrichon pratense</i>		16	5%	1.45
<i>Helictotrichon pubescens</i>		12	4%	4.24
<i>Helictotrichon sedenense</i>	Helsede	23	7%	0.30
<i>Helictotrichon sempervirens</i>		1	0%	2.32
<i>Helictotrichon versicolor</i>	Helvers	19	6%	0.30
<i>Helleborus foetidus</i>		1	0%	4.24
<i>Heracleum sphondylium</i>		7	2%	1.18
<i>Hieracium angustifolium</i>	Hieangu	23	7%	0.30
<i>Hieracium aurantiacum</i>		1	0%	0.61
<i>Hieracium cymosum</i>		5	2%	1.04
<i>Hieracium glanduliferum</i>	Hieglan	56	17%	1.40

Species name	Species code	Transects		SRA
		n	%	
<i>Hieracium lactucella</i>	Hielact	55	16%	1.07
<i>Hieracium murorum</i> aggr.	Hiemuro	26	8%	0.30
<i>Hieracium peletierianum</i>		2	1%	1.98
<i>Hieracium pilosella</i>	Hiepilo	55	17%	0.54
<i>Hieracium piloselloides</i>		5	2%	0.54
<i>Hieracium pilosum</i>		2	1%	0.35
<i>Hieracium prenanthoides</i>		5	2%	1.06
<i>Hieracium pseudopilosella</i>		2	1%	0.89
<i>Hieracium saussureoides</i>		1	0%	0.30
<i>Hieracium tomentosum</i>		8	2%	0.49
<i>Hieracium valdepiosum</i>		3	1%	0.30
<i>Hieracium villosum</i>		1	0%	1.27
<i>Hippocrepis comosa</i>	Hipcomo	39	12%	0.57
<i>Holcus lanatus</i>		3	1%	1.54
<i>Homogyne alpina</i>	Homalpi	35	11%	0.30
<i>Huperzia selago</i>		1	0%	2.02
<i>Hypericum maculatum</i>		13	4%	0.79
<i>Hypericum perforatum</i>		11	3%	0.48
<i>Hypericum richeri</i>	Hyprich	66	20%	0.30
<i>Hypochaeris maculata</i>		10	3%	1.15
<i>Hypochaeris radicata</i>		1	0%	0.77
<i>Hypochaeris uniflora</i>	Hypunif	25	8%	0.30
<i>Jasione montana</i>		1	0%	3.96
<i>Juncus articulatus</i>		2	1%	3.85
<i>Juncus filiformis</i>		1	0%	0.89
<i>Juncus jacquinii</i>		5	2%	2.59
<i>Juncus trifidus</i>	Juntrif	53	16%	4.71
<i>Juncus triglumis</i>		1	0%	0.30
<i>Juniperus communis</i>		6	2%	1.14
<i>Juniperus nana</i>	Junnana	40	12%	0.88
<i>Knautia arvensis</i>		11	3%	0.30
<i>Knautia dipsacifolia</i>		1	0%	1.52
<i>Knautia mollis</i>		10	3%	0.30
<i>Koeleria hirsuta</i>		1	0%	0.30
<i>Koeleria macrantha</i>		1	0%	1.60
<i>Koeleria pyramidata</i>		8	2%	2.21
<i>Koeleria vallesiana</i>		2	1%	1.10
<i>Lactuca perennis</i>		3	1%	0.30
<i>Larix decidua</i>		13	4%	1.12
<i>Laserpitium gallicum</i>		3	1%	1.32
<i>Laserpitium halleri</i>		3	1%	0.80
<i>Laserpitium latifolium</i>		16	5%	2.90
<i>Laserpitium siler</i>		3	1%	1.14
<i>Lathyrus heterophyllus</i>		2	1%	1.63
<i>Lathyrus pratensis</i>	Latprat	28	9%	3.28

3. Relationships between vegetation, environmental factors and soil carbon stocks
in alpine summer pastures

Species name	Species code	Transects		SRA
		n	%	
<i>Lathyrus sphaericus</i>		2	1%	2.49
<i>Lavandula angustifolia</i>		8	2%	1.28
<i>Leontodon autumnalis</i>		3	1%	1.81
<i>Leontodon crispus</i>		6	2%	5.05
<i>Leontodon helveticus</i>	Leohelv	77	24%	0.30
<i>Leontodon hirtus</i>		1	0%	2.51
<i>Leontodon hispidus</i>	Leohisp	89	27%	0.57
<i>Leontopodium alpinum</i>		9	3%	1.33
<i>Leucanthemopsis alpina</i>	Leualpi	21	6%	0.77
<i>Leucanthemum atratum</i> aggr.	Leuatra	19	6%	0.62
<i>Leucanthemum vulgare</i> aggr.	Leuvulg	56	17%	6.53
<i>Ligusticum mutellina</i>		17	5%	2.23
<i>Ligusticum mutellinoides</i>		6	2%	0.30
<i>Lilium bulbiferum</i>		4	1%	0.30
<i>Lilium martagon</i>		6	2%	0.53
<i>Linum alpinum</i>		7	2%	1.29
<i>Linum strictum</i>		7	2%	0.30
<i>Linum tenuifolium</i>		1	0%	0.30
<i>Listera ovata</i>		1	0%	1.41
<i>Lloydia serotina</i>		2	1%	1.10
<i>Loiseleuria procumbens</i>		7	2%	1.51
<i>Lolium multiflorum</i>		2	1%	1.91
<i>Lotus corniculatus</i>	Lotcorn	185	57%	5.35
<i>Luzula alpinopilosa</i>	Luzalpi	23	7%	1.22
<i>Luzula campestris</i> aggr.	Luzcamp	88	27%	2.76
<i>Luzula lutea</i>	Luzlute	44	14%	1.17
<i>Luzula luzuloides</i>		4	1%	2.42
<i>Luzula nivea</i>		13	4%	1.30
<i>Luzula sieberi</i>		16	5%	0.71
<i>Luzula spicata</i> aggr.	Luzspic	42	13%	0.61
<i>Maianthemum bifolium</i>		3	1%	0.30
<i>Malus domestica</i>		1	0%	2.44
<i>Medicago lupulina</i>		6	2%	0.30
<i>Medicago sativa</i>		1	0%	1.93
<i>Meum athamanticum</i>	Meuatha	36	11%	0.30
<i>Minuartia austriaca</i>		1	0%	1.19
<i>Minuartia capillacea</i>		3	1%	0.46
<i>Minuartia laricifolia</i>		4	1%	1.54
<i>Minuartia recurva</i>		1	0%	0.96
<i>Minuartia sedoides</i>		10	3%	0.80
<i>Minuartia verna</i>	Minvern	23	7%	43.12
<i>Molinia arundinacea</i>		1	0%	24.20
<i>Molinia caerulea</i>		3	1%	0.58
<i>Myosotis alpestris</i>	Myoalpe	69	21%	0.60
<i>Myosotis arvensis</i>		16	5%	0.30

Species name	Species code	Transects		SRA
		n	%	
<i>Myosotis ramosissima</i>		1	0%	0.30
<i>Myosotis sylvatica</i>		1	0%	0.30
<i>Myrrhis odorata</i>		1	0%	0.56
<i>Narcissus radiiflorus</i>		3	1%	13.68
<i>Nardus stricta</i>	Narstri	175	54%	0.30
<i>Nepeta nepetella</i>		1	0%	0.33
<i>Nigritella rhellicani</i>	Nigrhel	26	8%	2.04
<i>Odontites luteus</i>		1	0%	7.84
<i>Onobrychis montana</i>	Onomont	39	12%	0.76
<i>Onobrychis viciifolia</i>		1	0%	1.58
<i>Ononis cristata</i>		3	1%	1.20
<i>Ononis natrix</i>		5	2%	0.30
<i>Orchis mascula</i>		1	0%	0.30
<i>Orchis militaris</i>		1	0%	0.30
<i>Orchis tridentata</i>		4	1%	0.30
<i>Orchis ustulata</i>		7	2%	1.37
<i>Oreochloa seslerioides</i>		2	1%	1.02
<i>Ornithogalum umbellatum</i>	Ornumbe	35	11%	2.73
<i>Oxytropis campestris</i>		4	1%	0.96
<i>Oxytropis helvetica</i>		12	4%	0.39
<i>Oxytropis lapponica</i>		4	1%	3.05
<i>Oxytropis neglecta</i>		5	2%	1.56
<i>Paradisea liliastrum</i>		13	4%	0.34
<i>Parnassia palustris</i>		5	2%	0.30
<i>Pastinaca sativa</i>		1	0%	0.61
<i>Pedicularis cenisia</i>		7	2%	0.99
<i>Pedicularis comosa</i>		1	0%	0.30
<i>Pedicularis foliosa</i>		2	1%	0.61
<i>Pedicularis gyroflexa</i>	Pedgyro	37	11%	0.77
<i>Pedicularis kernerii</i>		7	2%	0.63
<i>Pedicularis rosea</i>		2	1%	0.64
<i>Pedicularis rostratospicata</i>	Pedrost	20	6%	0.44
<i>Pedicularis tuberosa</i>		5	2%	0.62
<i>Pedicularis verticillata</i>		3	1%	41.28
<i>Petasites hybridus</i>		1	0%	0.53
<i>Peucedanum oreoselinum</i>		2	1%	1.31
<i>Peucedanum ostruthium</i>	Peuostr	18	6%	0.89
<i>Phleum phleoides</i>		2	1%	2.68
<i>Phleum pratense</i>		4	1%	4.61
<i>Phleum rhaeticum</i>	Phlrhae	112	35%	0.91
<i>Phyteuma betonicifolium</i>	Phybeto	89	27%	2.53
<i>Phyteuma globulariifolium</i>	Phyglob	18	6%	1.23
<i>Phyteuma hemisphaericum</i>	Phyhemi	21	6%	1.19
<i>Phyteuma michelii</i>	Phymich	30	9%	0.85
<i>Phyteuma orbiculare</i>	Phyorbi	43	13%	0.38

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Species name	Species code	Transects		SRA
		n	%	
<i>Phyteuma ovatum</i>		5	2%	0.30
<i>Phyteuma scheuchzeri</i>		1	0%	0.62
<i>Phyteuma scorzonerifolium</i>		6	2%	0.30
<i>Phyteuma spicatum</i>		1	0%	0.30
<i>Picea abies</i>		1	0%	0.30
<i>Picris hieracioides</i>		1	0%	0.66
<i>Pimpinella major</i>		9	3%	1.36
<i>Pimpinella saxifraga</i>		14	4%	0.64
<i>Pinguicula alpina</i>		1	0%	0.30
<i>Pinguicula vulgaris</i>		1	0%	0.30
<i>Pinus mugo</i>		5	2%	0.30
<i>Pinus sylvestris</i>		3	1%	4.27
<i>Plantago alpina</i> aggr.	Plaalpi	130	40%	1.89
<i>Plantago atrata</i>		7	2%	3.27
<i>Plantago fuscescens</i>	Plafusc	32	10%	1.09
<i>Plantago lanceolata</i>	Plalanc	21	6%	0.91
<i>Plantago major</i>		8	2%	2.11
<i>Plantago media</i>	Plamedia	25	8%	0.39
<i>Platanthera bifolia</i>		4	1%	0.30
<i>Platanthera chlorantha</i>		1	0%	4.82
<i>Poa alpina</i>	Poaalpi	175	54%	3.00
<i>Poa annua</i> aggr.		9	3%	1.52
<i>Poa bulbosa</i>		1	0%	0.30
<i>Poa cenisia</i>		1	0%	3.42
<i>Poa chaixii</i>	Poachai	27	8%	0.30
<i>Poa minor</i>		1	0%	0.30
<i>Poa nemoralis</i>		3	1%	3.01
<i>Poa pratensis</i>	Poaprat	27	8%	2.33
<i>Poa trivialis</i>		6	2%	4.85
<i>Poa variegata</i>	Poavari	68	21%	0.51
<i>Polygala alpestris</i>	Polalpe	23	7%	0.30
<i>Polygala alpina</i>		1	0%	0.30
<i>Polygala amarella</i>		2	1%	1.79
<i>Polygala chamaebuxus</i>		3	1%	0.37
<i>Polygala vulgaris</i>	Polvulg	21	6%	0.30
<i>Polygonatum verticillatum</i>		2	1%	1.23
<i>Polygonum alpinum</i>		4	1%	0.30
<i>Polygonum aviculare</i>		1	0%	3.28
<i>Polygonum bistorta</i>	Polbist	85	26%	3.20
<i>Polygonum viviparum</i>	Polvivi	84	26%	0.30
<i>Populus tremula</i>		1	0%	0.30
<i>Potentilla alba</i>		2	1%	0.30
<i>Potentilla argentea</i>		2	1%	2.97
<i>Potentilla aurea</i>	Potaure	36	11%	2.83
<i>Potentilla crantzii</i>	Potcran	49	15%	3.37

Species name	Species code	Transects		SRA
		n	%	
<i>Potentilla erecta</i>	Poterec	51	16%	0.30
<i>Potentilla fruticosa</i>		1	0%	1.76
<i>Potentilla grandiflora</i>	Potgran	115	35%	0.97
<i>Potentilla intermedia</i>		2	1%	1.35
<i>Potentilla neumanniana</i>	Potneum	19	6%	1.64
<i>Potentilla reptans</i>		2	1%	0.53
<i>Potentilla rupestris</i>		3	1%	0.69
<i>Potentilla valderia</i>		2	1%	0.95
<i>Primula farinosa</i>		1	0%	0.30
<i>Primula hirsuta</i>		1	0%	2.24
<i>Primula pedemontana</i>		2	1%	0.74
<i>Primula veris</i>	Priveri	42	13%	0.30
<i>Pritzelago alpina</i>		1	0%	0.45
<i>Prunella grandiflora</i>		7	2%	1.83
<i>Prunella laciniata</i>		1	0%	1.28
<i>Prunella vulgaris</i>		9	3%	0.30
<i>Prunus avium</i>		1	0%	0.30
<i>Prunus domestica</i>		1	0%	0.30
<i>Prunus spinosa</i>		2	1%	0.36
<i>Pseudorchis albida</i>	Psealbi	28	9%	2.73
<i>Pteridium aquilinum</i>		5	2%	0.39
<i>Pulmonaria australis</i>		6	2%	0.30
<i>Pulmonaria officinalis</i>		1	0%	1.19
<i>Pulsatilla alpina</i>	Pulalpi	37	11%	0.30
<i>Pulsatilla halleri</i>		1	0%	0.90
<i>Pulsatilla vernalis</i>		7	2%	1.26
<i>Pyrola minor</i>		1	0%	0.30
<i>Pyrola rotundifolia</i>		1	0%	0.30
<i>Quercus pubescens</i>		1	0%	0.30
<i>Ranunculus aconitifolius</i>		3	1%	2.02
<i>Ranunculus acris</i>	Ranacri	18	6%	1.49
<i>Ranunculus bulbosus</i>		12	4%	2.07
<i>Ranunculus kuepferi</i>	Rankuep	53	16%	2.26
<i>Ranunculus montanus</i> aggr.	Ranmont	168	52%	0.37
<i>Ranunculus platanifolius</i>		2	1%	0.62
<i>Ranunculus repens</i>		1	0%	0.76
<i>Ranunculus seguieri</i>		1	0%	0.30
<i>Rhamnus alpina</i>		1	0%	0.30
<i>Rhamnus pumila</i>		1	0%	2.71
<i>Rhinanthus alectorolophus</i>		16	5%	1.15
<i>Rhinanthus glacialis</i>	Rhiglac	34	10%	0.92
<i>Rhodiola rosea</i>		3	1%	0.97
<i>Rhododendron ferrugineum</i>	Rhoferr	45	14%	0.30
<i>Rorippa islandica</i>		1	0%	0.42
<i>Rosa</i> aggr.	Rosaggr	25	8%	0.30

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		n	%	
<i>Rubus aggr.</i>		1	0%	1.93
<i>Rubus idaeus</i>		8	2%	0.71
<i>Rumex acetosa</i>	Rumacet	72	22%	0.59
<i>Rumex acetosella</i>		13	4%	2.15
<i>Rumex alpestris</i>		9	3%	6.42
<i>Rumex alpinus</i>		15	5%	1.35
<i>Rumex obtusifolius</i>		6	2%	2.15
<i>Rumex scutatus</i>		8	2%	0.74
<i>Sagina saginoides</i>	Sagsagi	20	6%	0.30
<i>Salix breviserrata</i>		2	1%	0.30
<i>Salix foetida</i>		1	0%	0.30
<i>Salix glaucosericea</i>		1	0%	0.30
<i>Salix hastata</i>		1	0%	0.30
<i>Salix helvetica</i>		2	1%	6.90
<i>Salix herbacea</i>	Salherb	35	11%	4.93
<i>Salix reticulata</i>		5	2%	5.08
<i>Salix retusa</i>		11	3%	2.30
<i>Salix serpyllifolia</i>		4	1%	2.52
<i>Salvia pratensis</i>		13	4%	0.92
<i>Sanguisorba minor</i>		13	4%	1.29
<i>Sanguisorba officinalis</i>		6	2%	0.50
<i>Saponaria ocymoides</i>		7	2%	1.99
<i>Satureja montana</i>		2	1%	0.30
<i>Saxifraga aizoides</i>		1	0%	1.55
<i>Saxifraga bryoides</i>		2	1%	0.30
<i>Saxifraga exarata</i> aggr.		2	1%	0.30
<i>Saxifraga oppositifolia</i>		1	0%	0.36
<i>Saxifraga paniculata</i>		9	3%	0.30
<i>Saxifraga purpurea</i>		3	1%	0.67
<i>Scabiosa columbaria</i> aggr.	Scacolu	42	13%	0.49
<i>Scilla bifolia</i>		4	1%	23.40
<i>Scirpus sylvaticus</i>		1	0%	0.30
<i>Scorzonera austriaca</i>		1	0%	0.30
<i>Scrophularia canina</i>		1	0%	1.41
<i>Scutellaria alpina</i>		5	2%	1.40
<i>Securigera varia</i>		3	1%	0.37
<i>Sedum acre</i>		4	1%	0.30
<i>Sedum album</i>		1	0%	1.87
<i>Sedum alpestre</i>		5	2%	0.49
<i>Sedum anacampseros</i>		17	5%	0.66
<i>Sedum rupestre</i> aggr.		6	2%	0.30
<i>Selaginella selaginoides</i>		2	1%	0.42
<i>Sempervivum arachnoideum</i>	Semarac	23	7%	1.38
<i>Sempervivum montanum</i>		11	3%	0.70
<i>Sempervivum tectorum</i>		12	4%	0.52

Species name	Species code	Transects		SRA
		n	%	
<i>Senecio doronicum</i>	Sendoro	29	9%	0.64
<i>Senecio incanus</i>	Seninca	33	10%	0.30
<i>Senecio jacobaea</i>		1	0%	0.30
<i>Senecio ovatus</i>		1	0%	0.30
<i>Senecio viscosus</i>		1	0%	1.40
<i>Seseli annuum</i>		1	0%	0.63
<i>Seseli libanotis</i>		4	1%	9.34
<i>Sesleria caerulea</i>	Sescaer	39	12%	1.13
<i>Sibbaldia procumbens</i>	Sibproc	22	7%	1.01
<i>Silene acaulis</i>	Silacau	37	11%	0.60
<i>Silene dioica</i>		4	1%	0.30
<i>Silene flos-cuculi</i>		1	0%	0.48
<i>Silene flos-jovis</i>		16	5%	0.30
<i>Silene latifolia</i>		1	0%	0.64
<i>Silene nutans</i>	Silnuta	59	18%	0.30
<i>Silene otites</i>		3	1%	0.37
<i>Silene rupestris</i>		9	3%	0.30
<i>Silene saxifraga</i>		1	0%	0.50
<i>Silene viscaria</i>		2	1%	1.25
<i>Silene vulgaris</i>	Silvulg	28	9%	1.27
<i>Soldanella alpina</i>	Solalpi	49	15%	0.55
<i>Solidago virgaurea</i>		16	5%	0.30
<i>Sorbus aria</i>		10	3%	0.30
<i>Sorbus aucuparia</i>		5	2%	0.98
<i>Stachys officinalis</i>		6	2%	0.69
<i>Stachys pradica</i>	Staprad	28	9%	0.63
<i>Stachys recta</i>		9	3%	1.09
<i>Stellaria graminea</i>		4	1%	0.97
<i>Stellaria holostea</i>		1	0%	1.57
<i>Stellaria media</i>		1	0%	20.33
<i>Stipa pennata</i> aggr.		3	1%	0.30
<i>Tanacetum vulgare</i>		2	1%	0.52
<i>Taraxacum laevigatum</i> s. l.		8	2%	1.03
<i>Taraxacum officinale</i> aggr.		13	4%	4.46
<i>Taraxacum officinale</i> s. l.	Taroffi	47	15%	0.30
<i>Tephroseris aurantiaca</i>		1	0%	5.85
<i>Teucrium chamaedrys</i>		13	4%	1.54
<i>Teucrium montanum</i>		4	1%	0.53
<i>Teucrium scorodonia</i>		4	1%	0.30
<i>Thalictrum aquilegiifolium</i>		1	0%	0.50
<i>Thalictrum minus</i> aggr.		6	2%	0.36
<i>Thesium alpinum</i>		7	2%	0.79
<i>Thesium linophyllum</i> aggr.		1	0%	0.45
<i>Thlaspi alpestre</i>	Thlalpe	19	6%	2.24
<i>Thymus serpyllum</i> aggr.	Thyserp	151	47%	0.30

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		n	%	
<i>Tofieldia calyculata</i>		1	0%	0.30
<i>Tragopogon dubius</i>		1	0%	0.45
<i>Tragopogon pratensis</i>		15	5%	0.30
<i>Traunsteinera globosa</i>		3	1%	6.49
<i>Trichophorum cespitosum</i>		2	1%	2.49
<i>Trifolium alpestre</i>	Trialpe	25	8%	12.62
<i>Trifolium alpinum</i>	Trialpi	108	33%	0.30
<i>Trifolium aureum</i>		1	0%	0.59
<i>Trifolium badium</i>	Tribadi	28	9%	3.57
<i>Trifolium hybridum</i>		1	0%	12.91
<i>Trifolium medium</i>		2	1%	1.70
<i>Trifolium montanum</i>	Trimont	30	9%	3.17
<i>Trifolium pallescens</i>		3	1%	1.22
<i>Trifolium pannonicum</i>		6	2%	2.16
<i>Trifolium pratense</i>	Triprat	147	45%	2.40
<i>Trifolium repens</i>	Trirepe	55	17%	6.03
<i>Trifolium thalii</i>	Trithal	34	10%	10.48
<i>Triglochin palustris</i>		1	0%	0.97
<i>Trinia glauca</i>		4	1%	0.80
<i>Trisetum distichophyllum</i>		1	0%	4.81
<i>Trisetum flavescens</i>	Triflav	51	16%	1.60
<i>Trollius europaeus</i>	Troeuro	30	9%	0.42
<i>Tulipa australis</i>		6	2%	1.19
<i>Tussilago farfara</i>		1	0%	1.25
<i>Urtica dioica</i>		15	5%	3.18
<i>Vaccinium gaultherioides</i>	Vacgaul	60	19%	2.36
<i>Vaccinium myrtillus</i>	Vacmyrt	68	21%	1.49
<i>Vaccinium vitis-idaea</i>		2	1%	3.16
<i>Valeriana celtica</i>		5	2%	0.30
<i>Valerianella locusta</i>		1	0%	0.52
<i>Veratrum album</i>	Veralbu	60	19%	0.88
<i>Verbascum densiflorum</i>		5	2%	0.30
<i>Verbascum lychnitis</i>		6	2%	0.38
<i>Verbascum thapsus</i>		6	2%	1.87
<i>Veronica allionii</i>	Veralli	53	16%	0.66
<i>Veronica alpina</i>	Veralpi	19	6%	0.30
<i>Veronica aphylla</i>		1	0%	0.30
<i>Veronica arvensis</i>		4	1%	2.28
<i>Veronica bellidioides</i>		5	2%	1.34
<i>Veronica chamaedrys</i>	Vercham	23	7%	0.47
<i>Veronica fruticulosa</i> aggr.		3	1%	1.50
<i>Veronica officinalis</i>	Veroffi	20	6%	0.30
<i>Veronica prostrata</i>		1	0%	0.70
<i>Veronica serpyllifolia</i>		4	1%	0.57
<i>Veronica verna</i>		1	0%	1.99

Species name	Species code	Transects		SRA
		n	%	
<i>Vicia cracca</i>		13	4%	0.30
<i>Vicia hirsuta</i>		1	0%	1.34
<i>Vicia onobrychioides</i>		2	1%	2.67
<i>Vicia sativa</i>		4	1%	1.44
<i>Vicia sepium</i>		2	1%	0.30
<i>Vicia villosa</i>		1	0%	0.30
<i>Vincetoxicum hirundinaria</i>		13	4%	0.30
<i>Viola arvensis</i>		1	0%	0.61
<i>Viola biflora</i>		9	3%	1.32
<i>Viola calcarata</i>	Viocalc	89	27%	2.00
<i>Viola canina</i>		4	1%	0.30
<i>Viola odorata</i>		1	0%	0.30
<i>Viola palustris</i>		1	0%	0.30
<i>Viola pinnata</i>		1	0%	0.52
<i>Viola riviniana</i>		3	1%	0.30
<i>Viola suavis</i>		2	1%	0.35
<i>Viola thomasiana</i>		5	2%	0.39
<i>Viola tricolor</i>		16	5%	0.30

Landolt E., Bäumler B., Erhardt A., Hegg O., Klotzli F., Lammler W., Nobis M., Rudmann-Maurer K., Schweingruber F.H., Theurillat J.-P. et al., 2010. *Flora Indicativa: Ökologische Zeigerwerte und Biologische Kennzeichen zur Flora der Schweiz und der Alpen = Ecological Indicator Values and Biological Attributes of the Flora of Switzerland and the Alps*, Editions des Conservatoire et Jardin Botaniques de la Ville de Genève & HauptVerlag: Bern, Switzerland, Stuttgart, Germany, Vienna, Austria, 2010, ISBN 978-3-258-07461-0.

4. Grassland productivity and forage quality of contrasting grassland types

Extended paper title: Topography, climate, species composition, and phenology affect forage yield and quality in alpine summer pastures (NW-Italy, Gran Paradiso National Park)

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Abstract

Summer pastures in the European Alps hold a high plant diversity and play a crucial role in providing high quality forage resources for grazing livestock. The main issue of their management is the optimal exploitation of the available forage in relation to environmental constraints. In this work, we characterized forage quantity and quality (i.e., digestibility and proximate composition) assessing the relative importance of climatic, topographic, and vegetation variables along the growing season through univariate and multivariate analyses. The cover of broadleaf 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 increasing cover of sedges and rushes and mean temperatures, respectively. Climatic variables (especially water deficit) and plant senescence 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. Specific valuable functional species pools could be maintained and enhanced through pastoral management which can thus represent an effective tool to face the ever more frequent incoming climatic adversities in the alpine environment.

Keywords: phenology, grassland, relative importance, RDA, digestibility, proximate composition, mountain

Introduction

Healthy food demand has continuously increased in Europe over the last years (Grunert, 2013). Grasslands play a crucial role in providing forage for high quality milk, meat, and other edible products in large areas around the world (Huyghe et al., 2014). In Europe, permanent grasslands cover 34% of the Utilised Agricultural Area (about 59.5 million hectares, Dillon, 2018). Among them, alpine long-term permanent grasslands host a high plant species diversity and support the provision of valuable forages (Ravetto Enri et al., 2017). For thousands of years, alpine summer pastures played a crucial role in the rural economy of temperate mountains since the forage produced by alpine pastures is generally the only feed for grazing livestock during summer (Sturaro et al., 2009; Battaglini et al., 2014). In these environments climate, topographic factors and vegetation composition can significantly differ even at a local scale (Ellenberg, 1988), affecting forage productivity and quality of pastures, along with plant phenology (Bätzing, 2003; Bätzing and Bartaletti, 2005; Wingler and Hennessy, 2016). Therefore, in order to optimize the exploitation of the available forage resources throughout the grazing season, pastoral management should consider the interaction among these factors.

Temperature and precipitation are well-known to significantly impact forage productivity and quality (Lascano et al., 2001; Dumont et al., 2015). Temperature affects potential evapotranspiration (Hargreaves and Samani, 1985) which is in turn balanced by precipitation (Wilcox et al., 2003). A marked negative balance between precipitation and evapotranspiration reduces the leaf-to-stem ratios and thus forage digestibility through an increased proportion of indigestible cell-wall fraction and concurrent reduction in non-structural carbohydrates (Buxton and Marten, 1989; Wilson, 1994; Buxton, 1996). Moreover, the ongoing climate changes emphasise 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 alpine ecosystems (Engler et al., 2011; Dullinger et al., 2012; Palombo et al., 2014).

In mountain areas the effects of climatic variables on vegetation are emphasized by the harsh environmental conditions due to slope, elevation and terrain roughness. Steep slopes speed up water runoff reducing water availability for plants and enhance evapotranspiration due to more direct and intense solar radiation; in steeper areas forage productivity is often reduced (Liu et al., 2020). Air temperature

decreases with increasing elevation (0.65 °C every 100 m) and affects the vegetation productivity (biomass production is generally lower) and the length of the growing season, which is shortened at higher elevation (Liu et al., 2015; Dongdong et al., 2020).

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 (Jeangros et al., 1999; Collomb et al., 2002; Roukos et al., 2011; Ravetto Enri et al., 2017; Renna et al., 2020). While in alpine environments previous studies focused on the differences among botanical families (Jeangros et al., 1999; Daccord et al., 2006) or vegetation communities (Andueza et al., 2016), only a few studies examined the proximate composition of single species (Marinas et al., 2003; Bovolenta et al., 2008). Therefore, a limited number of species were chemically characterised whereas alpine grasslands host several hundreds of different species (Landolt et al., 2010). With equal vegetation composition, the phenological stage has a noteworthy relevance on the forage availability and chemical features (Buxton and Marten, 1989; Nelson and Moser, 1994; Arzani et al., 2004), although evidence on species and grasslands of the Alps is still limited (Carrère et al., 2010).

In light of this background, the majority of research concerning the relations between climate, topography and vegetation composition on grassland productivity and quality has been carried out under manipulated conditions, in artificial settings, on species-poor temporary grassland or at the best on low-elevation permanent meadows. To our knowledge, no observation studies have been conducted on high-elevation species-rich pastures with the aim of assessing the relative importance of such variables in explaining forage yield and proximate composition. Therefore, we selected an area at the alpine belt of the Western-Italian Alps where the following specific objectives have been addressed:

- to improve the knowledge on how climate, topographic factors and plant community variables affect forage production and quality;
- to assess the relative importance of the different variables;
- to elucidate the relationships among forage yield and quality and vegetation characteristics in terms of plant species composition and plant community variables.

Materials and Methods

Study area

The research was carried out in 2019 and 2020 on 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, characterised by a continental climate (Braun-Blanquet, 1961; Ozenda, 1985). According to the two weather stations nearby (1700 m a.s.l.), mean annual temperature is +4.1°C and mean annual precipitation is about 700 mm (Mercalli and Cat Berro, 2003). The elevation of the valley ranges from 1830 to 3630 m a.s.l. of the peak *Punta Nera della Grivola*; grasslands are spread from the lower limit to about 2950 m a.s.l. Bedrock is largely composed by gneiss and micaschists, and to a lesser extent by serpentinite and calc-schists (Carletti, 2015; Le Bayon and Ballevre, 2006). Dominant soils are gravel and mainly nutrient-poor. The vegetation consists of semi-natural and natural grasslands rich in species, 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 in the upper parts of the valley.

Field surveys

Six different sites were selected within the alpine belt aiming at exploring a broad elevation and trophic variability among grasslands (Figure 4.1). In both the lower and the upper alpine belts (2200-2500 m a.s.l. and 2500-2800 m a.s.l., respectively; Ozenda, 1985), three fertility levels were identified, based on the overall vegetation composition, i.e. oligotrophic, mesotrophic and eutrophic grasslands (Pittarello et al., 2018), as detailed in table 4.1.

In spring 2019 a plot of 3.75 x 2.5 m at the lower alpine belt and 3.75 x 2 m at the upper one was set up for each vegetation community and excluded from grazing by fences. Each plot was equipped with temperature data-loggers (Hobo Onset Proseries, 1 hour time recording interval) at ground level, while daily precipitation was retrieved from the nearest meteorological station. Each vegetation community was surveyed with a point-intercept method applied at 5 cm-interval (Daget and Poissonet, 1971) along 1.25-m linear transects. The species list was completed by recording of all the other vascular plant species within a 50-cm buffer area around the transect. Surveys were carried out with three replicates, five times at the lower elevation and four times at the

higher one, where the growing season was shorter. The same sampling procedure was carried out in 2020. Overall, 162 vegetation surveys were carried out. Taxonomic nomenclature followed the Checklist of the Italian native vascular flora (Bartolucci et al., 2018).

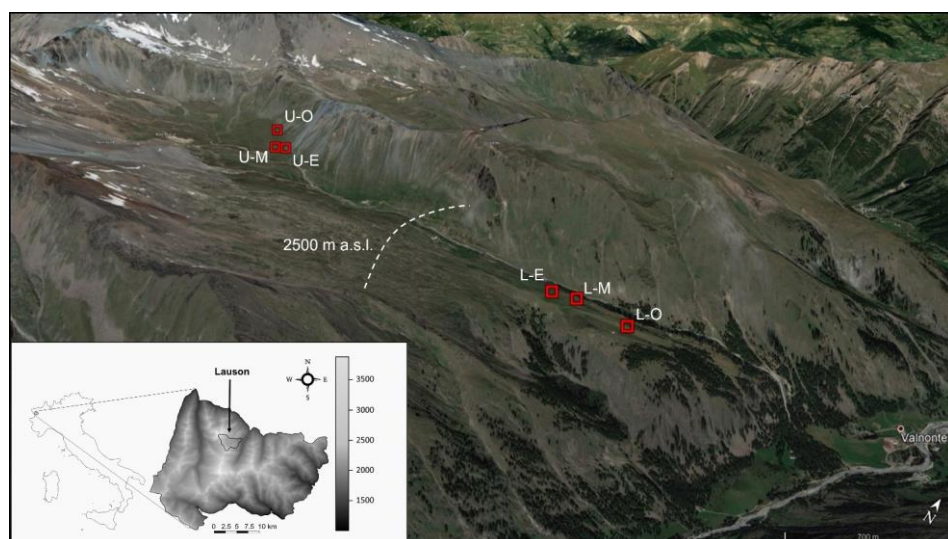


Figure 4.1. Representation of the Lauson valley (Cogne, Gran Paradiso National Park, NW-Italy) including the position of the investigated plots where: L, means lower alpine belt; U, upper alpine belt; O, oligotrophic vegetation; M, mesotrophic vegetation; and E, eutrophic vegetation.

Table 4.1. Description of the identified plots in terms of elevation belt, fertility level, dominant species, elevation, and slope. Taxonomic nomenclature followed the Italian vascular checklist (Bartolucci et al. 2018).

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

For each plant species recorded in the surveys, the frequency of occurrence, which is an estimate of species canopy cover (Probo et al., 2013; Perotti et al., 2018), was calculated. A cover of 0.3% was attributed to all occasional plant species observed in the buffer area (Tasser and Tappeiner, 2005). At each survey date the average plant phenological stage was recorded for each species according to the 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 x 0.50 m subplot (i.e. three samples per plot and date). The herbage mass was harvested afterwards, stored immediately in polyethylene bags at 4°C in a portable refrigerator and transported to the laboratory.

Forage analyses

Forage samples were oven-dried at 65°C for 48 hours and then weighed to compute yields (t ha^{-1}). The samples were then ground with a Cyclotec mill (Foss Tecator, Hoganas, Sweden, 1 mm screen) and analysed with near infrared reflectance spectroscopy technique (SpectraStar NIR Analyzer – Unity Scientific, Westborough, Massachusetts, U.S.A.) for proximate composition, namely neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), crude protein (CP), soluble sugars, and dry matter digestibility. Biomass, proximate composition and digestibility were considered as response variables in the statistical analyses.

Computation of explanatory variables

Topographic variables.

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

Eco-climatic variables.

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). Moreover, the mean temperatures between the date of the snowmelt and the date of the first survey and, subsequently, between adjacent survey dates, were recorded. 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, i.e. ΔPrET . Potential evapotranspiration was computed for each plot based on temperatures from the day of snowmelt, according to Hargreaves equation (Hargreaves and Samani 1985). Low values of ΔPrET were considered as an indicator of the water stress to which vegetation was subjected.

Plant community variables.

Each plant vascular species was assigned to one of the following species functional groups: i) sedges and rushes; ii) narrow-leaf grasses (species with leaves 1-3 mm large, Dorée, 1995); iii) broadleaf grasses (grasses with leaves larger than 4 mm, Dorée, 1995); iv) legumes; v) other species. Then, the total canopy cover of each functional group was calculated for every plot.

Statistical analyses

To assess the relative importance of topographic, eco-climatic and plant community variables on forage quantity and quality a GLMM (generalized linear mixed model) analysis was performed. Highly collinear variables (Pearson $r > |0.70|$) were excluded from the analysis. The 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) distribution family (best regression family based on 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 dates of survey nested in the six plots were considered as random factor to account for spatio-temporal autocorrelation. Significance was set at $p < 0.05$. 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 and 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.

Results

Climate and plant communities

During 2020, the growing season started about 10 days earlier compared to 2019 (15 May 2019 vs 5 May 2020). In 2020, the hottest daily mean temperatures were reached in the II decade of August, while in 2019 they were lower and recorded already in the III decades of June and July, respectively. Total rainfall during the two growing seasons was similar (9 mm less in 2020). Despite an intense event in the I decade of June (10/06/2019, 79 mm), total rainfall in 2019 was more evenly distributed across the growing season than in 2020. In 2020, most of the precipitation was concentrated in two periods at the beginning of the season (I decade of May and III decade of June), with a strong lack in July (67 and 15 mm respectively in July 2019 and 2020), in the middle of the growing season of alpine grasslands over treeline. Precipitation events occurred again in the II decade of August. In 2019 ΔPrET was characterised by a smoother decline throughout the season compared to 2020, with several brief changes of gradient according to rain events, almost absent in 2020 (Figure 4.2).

A total of 133 different vascular species was recorded in the six plots (see Appendix 1 for complete list of species). Among these, six were sedges and rushes, eight narrow-leaf grasses, 12 broadleaf grasses, 10 legumes, and 93 other species. Broadleaf grasses and other species were the dominant functional species pool in terms of species cover (Figure 4.3). 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*. Legumes were a minor species pool as well and did not overcome the 25% of cover (L-M plot).

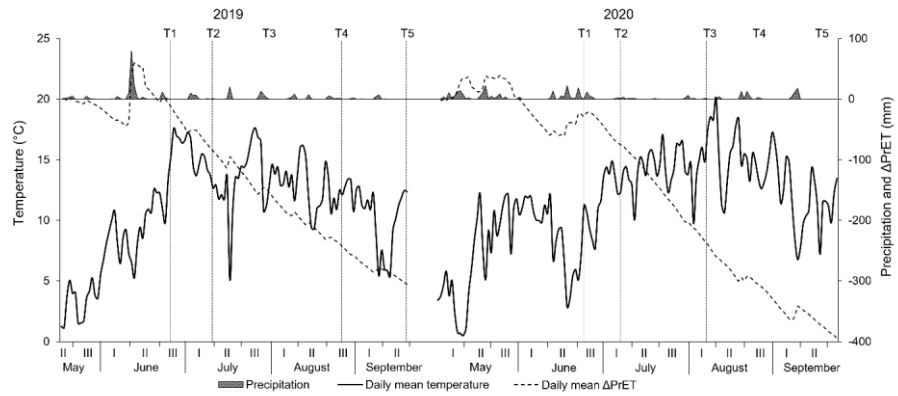


Figure 4.2. Distribution of daily mean temperature in °C, daily precipitation in mm and ΔPrET (water balance between precipitation and evapotranspiration) in mm across the growing seasons 2019 (left) and 2020 (right) from the day of snow melt in the Lauson valley. Months are subdivided in decades (I to III) and T1 to T5 represent the dates of survey in 2019 and 2020.

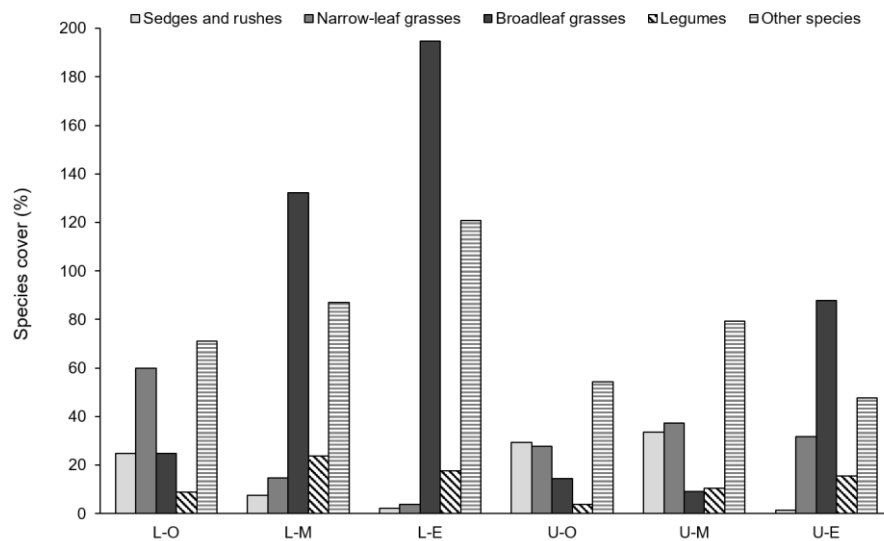


Figure 4.3. Cover (%) of the forage functional groups in the six plots where: L, means lower elevation belt; U, upper elevation belt; O, oligotrophic vegetation; M, mesotrophic vegetation; and E, eutrophic vegetation.

Forage yield and quality

The forage yield and quality in terms of biomass, proximate composition and digestibility are reported in table 4.2. 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 characterised 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 at 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 crude protein was higher 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 crude protein 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 characterised by a high digestibility (around 75% at T1) while low mean values were found in plots L-O and U-M (around 45% at T5).

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

Since all the explanatory variables were not correlated each other ($r < |0.70|$), they were all included in the GLMM model (Table 4.3). The grassland biomass reduced mainly as elevation and slope increased ($\beta = -0.58$; $\beta = -0.38$, respectively), while a high broadleaf grass cover resulted in a higher biomass ($\beta = 0.42$). Increasing cover of sedges and rushes and mean temperatures enhanced biomass production but with a lower relative importance compared to other significant variables. ΔPrET contribution was weak, while plant phenology, cover of narrow-leaf grasses, legumes and other species had no significant role in biomass production. Decreasing ΔPrET (i.e., toward drought conditions) and increasing phenology 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 with relatively lower importance. Among plant community variables, only the cover of the other species influenced significantly ADF content with a slight lowering effect ($\beta = -0.03$).

Table 4.2. Average (summers 2019-2020) mean and standard error (s.e.) of forage productivity and proximate composition of the investigated vegetation plots of the Lauson valley where: L, means lower alpine belt; U, upper alpine belt; O, oligotrophic vegetation; M, mesotrophic vegetation; and E, eutrophic vegetation. NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin.

PLOT		Biomass (t ha ⁻¹)		NDF (g kg ⁻¹)		ADF (g kg ⁻¹)		ADL (g kg ⁻¹)	
		mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
L-O	T1	0.5	0.10	417.1	37.07	202.5	20.30	36.1	3.88
	T2	0.5	0.06	434.2	13.96	212.6	6.56	39.4	2.64
	T3	0.4	0.09	476.6	19.73	240.2	9.66	45.7	2.30
	T4	0.5	0.10	534.3	32.79	279.4	19.49	54.8	1.77
	T5	0.4	0.05	615.7	33.15	329.8	15.61	64.9	2.05
L-M	T1	0.8	0.17	440.5	17.15	194.7	7.71	27.1	0.78
	T2	1.0	0.13	431.8	8.93	200.3	3.77	29.5	0.87
	T3	0.7	0.09	456.7	17.35	234.1	8.53	43.4	1.07
	T4	1.1	0.21	526.3	15.30	274.3	6.64	52.9	1.26
	T5	0.8	0.14	605.9	8.20	323.4	4.14	63.6	1.38
L-E	T1	1.8	0.49	438.9	14.29	199.1	6.78	27.5	1.42
	T2	3.3	0.55	459.4	10.57	214.0	5.74	30.1	0.66
	T3	3.0	0.34	480.4	10.05	232.8	6.69	36.3	1.51
	T4	2.8	0.34	527.5	23.88	263.0	14.91	43.5	3.44
	T5	2.3	0.20	564.2	23.53	286.4	12.27	51.8	2.80
U-O	T2	0.2	0.03	365.8	12.38	174.2	4.83	28.2	0.51
	T3	0.2	0.03	431.1	36.55	217.6	18.26	39.3	3.92
	T4	0.3	0.09	468.5	42.67	244.2	23.37	46.7	3.30
	T5	0.1	0.02	570.8	23.71	300.0	14.59	58.9	4.19
U-M	T2	0.2	0.04	471.4	16.58	237.6	12.37	46.8	4.16
	T3	0.4	0.11	496.3	23.83	264.9	19.59	56.3	5.29
	T4	0.5	0.19	523.6	19.39	283.6	10.62	62.8	2.82
	T5	0.3	0.05	624.1	14.38	346.2	12.03	74.5	4.06
U-E	T2	0.4	0.05	421.2	13.08	177.9	5.06	25.5	1.36
	T3	0.4	0.09	462.3	13.73	218.7	2.84	41.9	3.54
	T4	0.6	0.12	475.0	10.90	218.3	4.27	44.3	1.88
	T5	0.3	0.08	566.8	22.72	265.7	16.00	50.8	3.52

cont.

Table 4.2. cont.

		Crude Protein		Soluble sugars		Digestibility	
		(g kg ⁻¹)		(g kg ⁻¹)		(%)	
PLOT		mean	s.e.	mean	s.e.	mean	s.e.
L-O	T1	133.1	8.02	114.4	21.57	67.0	1.32
	T2	118.8	5.18	108.5	13.66	64.9	0.92
	T3	97.7	5.27	99.3	9.49	59.7	1.38
	T4	90.0	3.69	66.4	6.59	53.9	2.62
	T5	68.5	5.57	41.9	6.03	47.6	1.66
L-M	T1	159.7	15.01	129.4	22.62	72.2	0.73
	T2	134.7	8.41	134.8	10.12	72.1	0.86
	T3	98.5	3.39	108.8	5.06	64.0	0.86
	T4	88.8	3.45	79.1	7.25	58.7	1.30
	T5	66.3	5.25	45.7	4.48	51.7	0.55
L-E	T1	178.9	25.23	98.2	23.15	73.3	0.95
	T2	149.0	12.99	110.4	17.44	71.9	0.63
	T3	125.0	16.59	100.6	12.04	68.6	1.65
	T4	108.6	14.18	77.5	6.39	63.7	3.04
	T5	92.2	4.82	59.0	6.02	60.6	2.01
U-O	T2	142.7	9.69	117.6	7.17	70.1	0.98
	T3	99.3	15.66	100.2	10.65	63.8	1.14
	T4	84.8	8.10	89.0	4.59	58.6	1.47
	T5	56.3	3.07	52.3	12.21	52.4	2.66
U-M	T2	115.8	3.13	98.1	8.76	65.6	2.88
	T3	96.0	4.73	87.2	12.01	60.3	2.99
	T4	76.8	3.59	74.7	7.93	56.5	2.03
	T5	58.1	3.20	37.1	8.00	47.3	2.44
U-E	T2	130.6	8.83	148.4	14.81	76.4	0.71
	T3	92.8	4.37	134.7	8.80	67.4	1.09
	T4	87.8	5.93	146.4	8.81	67.9	0.61
	T5	72.5	5.56	138.1	17.80	62.4	2.20

The increase in slope and cover of sedges and rushes were weakly significant in enhancing ADL content while increasing cover of broadleaf grasses and narrow-leaf grasses lowered it in turn. Decreasing ΔPrET ($\beta = 0.20$) and increasing phenology ($\beta = -0.10$) negatively affected crude protein with a ten-fold higher relative importance compared to other significant variables. Elevation, slope, mean temperatures and increasing broadleaf grasses cover negatively influenced crude protein content. Soluble sugars showed a positive relation with elevation and the cover of broadleaf grasses ($\beta = 0.24$ and 0.23 , respectively), while negative relationships were observed with ΔPrET and plant phenology. The factors affecting digestibility were, in order of importance, ΔPrET , phenology, elevation (weakly significant), the cover of sedges and rushes (negatively) and the cover of legumes (positively).

Table 4.3. Results of Generalized Linear Mixed Model (GLMM) showing the effects of eco-climatic (mean temperature and ΔPrET) 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. Asterisks and cross-shaped symbol represent statistical significance: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; †, $p < 0.1$ weak significant; n.s., not significant ($p \geq 0.05$). NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin; ΔPrET , water balance between precipitation and evapotranspiration.

Variables	Biomass ¹			NDF ²			ADF ²			ADL ²		
	Rank	β	Sig.	Rank	β	Sig.	Rank	β	Sig.	Rank	β	Sig.
Intercept		-0.54	***		-0.03	n.s.		-1.14	***		-0.2	**
Eco-climatic												
Mean temperature	5	0.15	**		0	n.s.		-0.01	n.s.		-0.03	n.s.
ΔPrET	6	0.09	†	1	-0.18	***	1	-0.15	***	1	-0.29	***
Topographic												
Slope	3	-0.38	*		0	n.s.		0.02	n.s.	3	0.16	†
Elevation	1	-0.58	***	2	-0.11	†		-0.09	n.s.		-0.02	n.s.
Plant community												
Sedges and rushes	4	0.18	***		0.03	n.s.		0.02	n.s.	5	0.05	†
Narrow-leaf grasses		0.06	n.s.		0.00	n.s.		0.00	n.s.	6	-0.05	†
Broadleaf grasses	2	0.42	***		0.03	n.s.		-0.02	n.s.	4	-0.12	*
Legumes		0.05	n.s.	5	-0.03	*		-0.01	n.s.		0.01	n.s.
Other species		-0.02	n.s.	4	-0.06	***	3	-0.03	*		0.01	n.s.
Phenology		-0.01	n.s.	3	0.08	***	2	0.09	***	2	0.18	***

cont.

Table 4.3. cont.

Variables	Crude Protein ²			Soluble sugars ²			Digestibility ²		
	Rank	β	Sig.	Rank	β	Sig.	Rank	β	Sig.
Intercept		-2.19	***		-2.3	***		0.54	***
Eco-climatic									
Mean temperature	6	-0.06	**		0.03	n.s.		-0.02	n.s.
Δ PrET	1	0.2	***	4	0.1	*	1	0.18	***
Topographic									
Slope	3	-0.08	**		0.08	n.s.		0.07	n.s.
Elevation	4	-0.08	**	1	0.24	*	3	-0.07	†
Plant community									
Sedges and rushes		-0.03	n.s.		-0.03	n.s.	4	-0.04	**
Narrow-leaf grasses		-0.01	n.s.		0.03	n.s.		0.00	n.s.
Broadleaf grasses	5	-0.08	*	2	0.23	***		0.03	n.s.
Legumes		0.02	n.s.		-0.01	n.s.	5	0.03	*
Other species		-0.01	n.s.		0.03	n.s.		0.01	n.s.
Phenology	2	-0.1	***	3	-0.18	***	2	-0.11	***

¹Family: Gamma

²Family: Beta

The RDA ordination was statistically significant ($p < 0.001$, $R^2_{adj} = 0.56$) and 78.2% and 7.6% of the total variance were explained by the first and second axes, respectively (Figure 4.4). The plant species were separated along the first axis according mainly to their digestibility. Crude protein and soluble sugar content (on the left side of the graph) opposed to fibre content (on the right), with biomass 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.), broadleaf 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* Ser. ex Gaudin, *Nardus stricta* L.) and sedges (e.g. *Carex sempervirens* Vill.) were linked to a

higher fibre content.

The species were distributed on the second axis along an altitudinal 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.

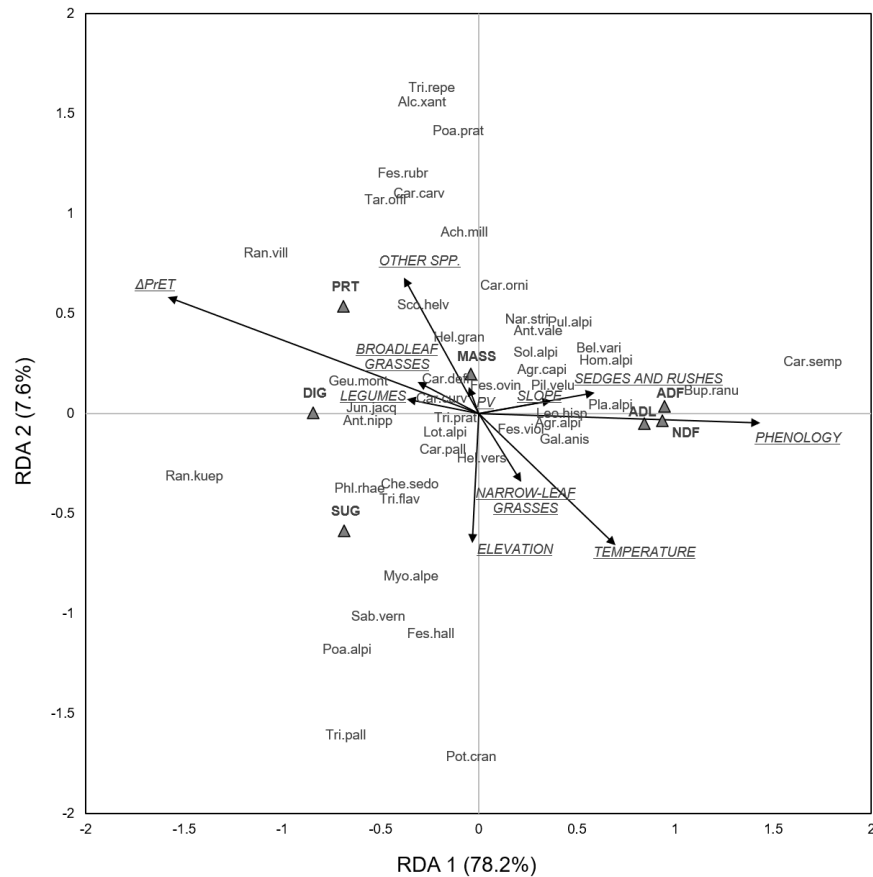


Figure 4.4. RDA ordination bi-plot showing the relations between forage yield and quality variables (triangles) and plant species composition (species are identified by codes; full names are provided in Appendix 1). Eco-climatic variables, phenology, topography and forage functional groups are projected as passive variables (arrows). MASS, forage yield; DIG, dry matter digestibility; PRT, crude protein; SUG, soluble sugars; NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin; ΔPrET, water balance between precipitation and evapotranspiration.

Discussion

Our research provided novel information concerning the relative importance of eco-climatic, topographic, and plant community variables in affecting pasture yield and forage quality in alpine pastures. Several other studies have been carried out with this aim in manipulated conditions on mono-specific or species-poor temporary grasslands or in low elevation meadows, varying mainly single factors and achieving contrasting outcomes (Cantarel et al., 2013; Bai et al., 2013; Sanaullah et al., 2014; Dumont et al., 2015; Peratoner et al., 2020). Our study should be regarded as one of the first 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 ΔPrET , 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 (Table 4.3). Specifically, water balance was particularly relevant, even if with differing magnitudes when compared to the effects exerted by the covers of functional species pools. Indeed, for fibre contents the covers of functional species pools had no more than half of the relative importance of ΔPrET as for broadleaf grass cover on ADL while such ratio did not exceed one sixth in the case of legume cover on NDF. Grasses cover decreased with elevation being replaced by other species, which is common in alpine pastures (Körner, 2003). However, their role in relation to productivity was of major importance. In particular, the cover of broadleaf 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. 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 alpine 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 (Körner et al., 1989; Fabbro and Körner, 2003). 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 quality (Jeangros et al., 1999). Concerning legumes, despite their low cover in our study area, they played a significant role in determining digestibility, 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 recognised 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 broadleaved) did not significantly affect forage digestibility even if broadleaf grasses had a major role in explaining soluble sugars content (Table 4.3) which are the primary source of the readily available energy for rumen fermentation. Therefore, the increase of broadleaf grasses cover should be regarded as a target to obtain valuable forages with high yield and sugars concentrations and low lignin content through pastoral management (Perotti et al., 2018).

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. 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 and Jarrige, 1981; Moore and Jung, 2001). This was confirmed by our study, as phenology impacted fibre contents, crude protein, and digestibility with a magnitude second only to ΔPrET , highlighting the importance of the choice of the grazing period for maximizing the exploitation of forage resources. Similar findings were observed 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. Further, the position of temperature, ΔPrET and

phenology in Figure 4.4 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 towards the chemical parameters related to fibre (NDF, ADF, and ADL), while legumes, broadleaf 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 broadleaf grass *Agrostis capillaris* L. was positioned close to fibre fractions, far from most of the other broadleaf 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 jacquinii* 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. 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 little investigations on a limited number of species has so far been carried out (Marinas et al., 2003; Bovolenta et al., 2008).

Despite the more complex interactions between factors that occur in natural settings compared to manipulated experiments, the statistical analysis provided clear information about the primary role of eco-climatic variables and in particular of water availability and plant phenology in affecting forage yield and quality. Our study also provided additional information about the effects of vegetation composition of alpine grassland ecosystems characterised by high species diversity on forage features. Particularly, water balance strongly impacted forage productivity and proximate composition of summer pastures, depending on species 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. However, pastoral management would represent a suitable tool for counteracting such climatic hazards. Indeed, pastoral practices in the alpine environment can increase the cover of some functional species

pools to the detriment of others. It is already recognised that the management of livestock grazing and faecal and urine deposition can modify the soil fertility inputs and outputs and related botanical composition (Pittarello et al., 2016; Perotti et al., 2018). Increasing cover of broadleaf grasses, legumes or other species associated to a decrease 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.

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Annex 4.A

List of the plant species recorded in the botanical transects, with the corresponding taxon code (whether showed in the graphical result of the RDA, Figure 4.4), the functional pool of species and the average percentage cover per plot where: L, means lower alpine belt; U, upper alpine belt; O, oligotrophic vegetation; M, mesotrophic vegetation; and E, eutrophic vegetation. Taxonomic nomenclature followed the Italian vascular checklist (Bartolucci et al. 2018).

Taxon	Taxon code	Functional pool	Mean cover %					
			L-O	L-M	L-E	U-O	U-M	U-E
<i>Achillea millefolium</i> aggr.	Ach.mill	Other spp.	-	6.7	21.6	-	-	-
<i>Achillea nana</i> L.		Other spp.	-	-	-	0.3	-	0.3
<i>Agrostis alpina</i> Scop.	Agr.alpi	Narrow-leaf grasses	8.0	-	-	6.3	20.1	6.4
<i>Agrostis capillaris</i> L.	Agr.capi	Broadleaf grasses	5.9	6.7	31.6	-	-	6.3
<i>Agrostis schraderiana</i> Bech.	Agr.schr	Broadleaf grasses	-	4.0	-	1.8	-	17.3
<i>Ajuga pyramidalis</i> L.		Other spp.	2.1	-	-	-	-	-
<i>Alchemilla pentaphyllea</i> L.		Other spp.	-	-	-	1.0	-	-
<i>Alchemilla xanthochlora</i> aggr.	Alc.xant	Other spp.	6.3	16.9	68.3	-	1.2	0.3
<i>Androsace adfinis</i> subsp. <i>puberula</i> (Jord. & Fourr.) Kress		Other spp.	-	-	-	1.2	0.6	0.3
<i>Anemonoides baldensis</i> (L.) Galasso, Banfi & Soldano		Other spp.	0.3	-	-	-	-	-
<i>Antennaria dioica</i> (L.) Gaertn.		Other spp.	-	4.0	-	3.7	7.2	-
<i>Anthoxanthum odoratum</i> subsp. <i>nipponicum</i> (Honda) Tzvelev	Ant.nipp	Broadleaf grasses	8.0	24.6	6.3	9.0	4.2	1.3
<i>Anthriscus sylvestris</i> (L.) Hoffm.		Other spp.	1.8	0.3	-	-	-	-
<i>Anthyllis vulneraria</i> subsp. <i>valesiaca</i> (Beck) Guyot	Ant.vale	Legumes	2.3	-	-	-	1.9	-
<i>Arabis ciliata</i> Clairv.		Other spp.	-	0.9	-	-	-	-
<i>Arnica montana</i> L.		Other spp.	3.2	1.5	-	-	-	-

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<i>Astrantia minor</i> L.		Other spp.	0.3	-	-	-	-	-
<i>Bartsia alpina</i> L.		Other spp.	0.3	0.3	-	-	-	-
<i>Bellardiochloa variegata</i> (Lam.) Kerguelén	Bel.vari	Narrow-leaf grasses	15.5	15.1	-	-	0.3	5.5
<i>Biscutella laevigata</i> L.		Other spp.	0.9	-	-	-	-	-
<i>Bistorta officinalis</i> Delarbre		Other spp.	0.3	-	-	-	-	-
<i>Bistorta vivipara</i> (L.) Delarbre		Other spp.	0.3	2.2	-	-	-	-
<i>Botrychium lunaria</i> (L.) Sw.		Other spp.	0.9	1.7	0.3	-	0.5	0.3
<i>Bupleurum ranunculoides</i> L.	Bup.ranu	Other spp.	0.3	-	-	-	4.9	-
<i>Campanula scheuchzeri</i> Vill.		Other spp.	1.5	0.3	2.6	2.1	-	0.3
<i>Cardamine alpina</i> Willd.		Other spp.	-	-	-	0.3	-	-
<i>Carduus defloratus</i> L.	Car.defl	Other spp.	1.5	3.1	8.1	0.3	-	-
<i>Carex curvula</i> All.	Car.curv	Sedges & rushes	-	-	-	24.3	2.8	2.2
<i>Carex foetida</i> All.		Sedges & rushes	-	-	-	0.3	-	-
<i>Carex ornithopoda</i> Willd.	Car.orni	Sedges & rushes	11.5	6.2	-	-	-	-
<i>Carex pallescens</i> L.	Car.pall	Sedges & rushes	-	8.3	16.0	-	-	-
<i>Carex sempervirens</i> Vill.	Car.semp	Sedges & rushes	11.7	7.9	9.7	0.3	31.8	1.0
<i>Carlina acaulis</i> L.		Other spp.	1.5	2.5	-	-	-	-
<i>Carum carvi</i> L.	Car.carv	Other spp.	-	2.5	7.3	-	-	-
<i>Cerastium arvense</i> L. subsp. <i>strictum</i> Gaudin		Other spp.	-	1.5	0.3	0.3	1.1	0.5
<i>Cerastium fontanum</i> Baumg.		Other spp.	-	0.9	2.3	-	-	-
<i>Cherleria sedoides</i> L.	Che.sedo	Other spp.	-	-	-	12.0	-	-
<i>Coeloglossum viride</i> (L.) Hartm.		Other spp.	2.1	0.3	-	-	0.3	-
<i>Crocus vernus</i> (L.) Hill		Other spp.	2.5	3.2	-	-	-	-
<i>Dactylis glomerata</i> L.		Broadleaf grasses	-	-	9.5	-	-	-
<i>Draba aizoides</i> L.		Other spp.	-	-	-	0.8	2.0	0.3
<i>Erigeron atticus</i> Vill.		Other spp.	1.2	0.9	-	-	-	-
<i>Erigeron uniflorus</i> L.		Other spp.	-	-	-	0.3	1.5	0.3

<i>Euphorbia cyparissias</i> L.		Other spp.	3.8	-	-	-	-	-
<i>Euphrasia alpina</i> Lam.		Other spp.	0.3	-	-	-	-	-
<i>Euphrasia minima</i> Jacq. ex DC.		Other spp.	0.3	-	-	0.3	-	-
<i>Festuca halleri</i> aggr.	Fes.hall	Narrow-leaf grasses	-	-	-	23.6	20.2	25.1
<i>Festuca luedii</i> (Markgr.-Dann.) Foggi, Gr. Rossi, Parolo & Wallossek		Narrow-leaf grasses	4.0	-	-	-	-	-
<i>Festuca ovina</i> aggr.	Fes.ovin	Narrow-leaf grasses	7.8	-	-	-	-	-
<i>Festuca rubra</i> L. subsp. <i>commutata</i> (Gaudin) Markgr.-Dann.	Fes.rubr	Broadleaf grasses	19.2	47.5	72.1	-	-	-
<i>Festuca violacea</i> Ser. ex Gaudin	Fes.viol	Narrow-leaf grasses	41.5	2.7	-	2.3	6.8	5.5
<i>Gagea fragifera</i> (Vill.) Ehr. Bayer & G. López		Other spp.	-	-	-	-	4.0	0.3
<i>Galium anisophyllum</i> Vill.	Gal.anis	Other spp.	1.1	6.5	5.6	0.3	0.3	0.5
<i>Gentiana brachyphylla</i> Vill.		Other spp.	-	0.3	-	0.6	1.9	1.4
<i>Gentiana punctata</i> L.		Other spp.	4.0	2.5	-	-	-	-
<i>Gentiana verna</i> L.		Other spp.	0.3	2.1	-	0.3	2.5	1.2
<i>Gentianella ramosa</i> (Hegetschw.) Holub		Other spp.	0.3	0.3	-	-	0.8	-
<i>Geum montanum</i> L.	Geu.mont	Other spp.	0.3	0.3	-	28.5	2.8	2.7
<i>Helianthemum nummularium</i> subsp. <i>grandiflorum</i> (Scop.) Schinz & Thell.	Hel.gran	Other spp.	15.8	5.7	-	-	-	-
<i>Helictochloa versicolor</i> (Vill.) Romero Zarco	Hel.vers	Broadleaf grasses	7.6	-	-	1.3	3.8	-
<i>Hieracium prenanthoides</i> Vill.		Other spp.	0.3	-	-	-	-	-
<i>Hippocrepis comosa</i> L.		Legumes	-	-	-	-	8.1	-
<i>Homogyne alpina</i> (L.) Cass.	Hom.alpi	Other spp.	4.5	1.6	-	-	-	-
<i>Hornungia alpina</i> subsp. <i>brevicaulis</i> (Spreng.) O. Appel		Other spp.	-	-	-	1.1	-	-
<i>Jacobaea incana</i> (L.) Veldkamp aggr.		Other spp.	-	-	-	0.3	-	-
<i>Juncus jacquinii</i> L.	Jun.jacq	Sedges & rushes	5.2	-	-	10.2	-	-
<i>Juncus trifidus</i> L.		Sedges & rushes	7.7	-	-	11.1	-	-

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<i>Koeleria macrantha</i> (Ledeb.) Schult.		Narrow-leaf grasses	0.3	-	-	-	-	-
<i>Leontodon hispidus</i> L.	Leo.hisp	Other spp.	8.5	2.8	-	0.3	-	-
<i>Leucanthemum vulgare</i> (Vaill.) Lam.		Other spp.	4.9	-	-	-	-	-
<i>Lotus corniculatus</i> subsp. <i>alpinus</i> (DC.) Rothm.	Lot.alpi	Legumes	1.6	4.5	-	3.9	5.4	3.2
<i>Luzula lutea</i> (All.) DC.		Sedges & rushes	1.4	-	-	-	-	0.3
<i>Luzula spicata</i> (L.) DC.		Sedges & rushes	4.2	0.3	-	2.3	0.5	0.8
<i>Luzula sudetica</i> aggr.		Sedges & rushes	3.4	1.5	0.3	-	-	0.3
<i>Myosotis alpestris</i> F. W. Schmidt	Myo.alpe	Other spp.	0.7	2.1	-	0.9	1.3	2.3
<i>Nardus stricta</i> L.	Nar.stri	Narrow-leaf grasses	-	7.2	7.4	-	-	-
<i>Nigritella rhellicani</i> Teppner & E. Klein		Other spp.	-	-	-	-	0.3	-
<i>Noccaea virens</i> (Jord.) F.K. Mey.		Other spp.	0.3	0.3	-	-	-	0.3
<i>Omalotheca supina</i> (L.) DC.		Other spp.	-	-	-	0.3	-	-
<i>Omalotheca sylvatica</i> (L.) Sch. Bip. & F.W. Schultz		Other spp.	-	4.0	-	-	-	-
<i>Pachypleurum</i> <i>mutellinoides</i> (Crantz) Holub		Other spp.	-	-	-	0.8	-	0.3
<i>Phleum rhaeticum</i> (Humphries) Rauschert	Phl.rhae	Broadleaf grasses	7.4	31.8	47.1	6.9	8.0	59.0
<i>Pilosella glacialis</i> (Reyn. ex Lachen.) F.W. Schultz & Sch.Bip.		Other spp.	-	-	-	-	0.3	-
<i>Pilosella lactucella</i> (Wallr.) P. D. Sell & C. West		Other spp.	0.3	2.2	2.9	-	-	-
<i>Pilosella velutina</i> (Hegetschw.) F.W. Schultz & Sch. Bip.	Pil.velu	Other spp.	0.3	0.3	-	6.9	5.7	-
<i>Plantago alpina</i> L.	Pla.alpi	Other spp.	12.4	13.1	-	-	35.7	9.9
<i>Plantago media</i> L.		Other spp.	0.3	0.3	4.0	-	-	-
<i>Poa alpina</i> L.	Poa.alpi	Broadleaf grasses	2.3	6.9	5.1	2.7	2.1	11.7
<i>Poa pratensis</i> L.	Poa.prat	Broadleaf grasses	4.0	2.9	39.1	-	-	-
<i>Polygala alpina</i> (Poir. ex DC.) Steud.		Other spp.	1.5	2.0	-	0.3	0.8	0.3
<i>Potentilla crantzii</i> (Crantz) Beck ex Fritsch	Pot.cran	Other spp.	1.0	3.8	0.3	0.3	7.6	14.1

<i>Potentilla grandiflora</i> L.		Other spp.	-	2.6	-	-	-	-
<i>Pulsatilla alpina</i> (L.) Delarbre	Pul.alpi	Other spp.	2.5	0.3	-	0.3	7.3	-
<i>Ranunculus kuepferi</i> Greuter & Burdet	Ran.kuep	Other spp.	-	-	-	8.5	10.9	14.5
<i>Ranunculus villarsii</i> DC.	Ran.vill	Other spp.	3.3	17.6	13.9	-	-	4.0
<i>Rumex arifolius</i> All.		Other spp.	-	0.3	0.3	-	-	-
<i>Sabulina verna</i> (L.) Rchb.	Sab.vern	Other spp.	-	-	-	3.7	4.3	5.2
<i>Scorzoneroidea helvetica</i> (Mérat) Holub	Sco.helv	Other spp.	7.4	6.6	7.3	0.3	0.3	-
<i>Sedum alpestre</i> Vill.		Other spp.	-	-	-	0.3	-	-
<i>Selaginella selaginoides</i> (L.) P. Beauv. ex Schrank & Mart.		Other spp.	1.7	-	2.2	-	-	-
<i>Sempervivum arachnoideum</i> L.		Other spp.	-	-	-	0.3	1.6	0.8
<i>Sempervivum montanum</i> L.		Other spp.	-	-	-	0.9	-	0.3
<i>Sesleria caerulea</i> (L.) Ard.		Broadleaf grasses	8.6	-	-	-	-	-
<i>Sibbaldia procumbens</i> L.		Other spp.	-	-	-	1.6	1.7	0.9
<i>Silene acaulis</i> subsp. <i>bryoides</i> (Jord.) Nyman		Other spp.	-	-	-	0.3	-	-
<i>Silene nutans</i> L.		Other spp.	2.9	-	-	-	-	-
<i>Soldanella alpina</i> L.	Sol.alpi	Other spp.	5.5	2.7	3.2	-	-	-
<i>Solidago virgaurea</i> subsp. <i>minuta</i> (L.) Arcang.		Other spp.	-	0.3	-	-	-	-
<i>Taraxacum officinale</i> aggr.	Tar.offi	Other spp.	4.2	-	3.6	-	-	0.3
<i>Taraxacum</i> sect. <i>Alpina</i> G.E.Haglund		Other spp.	0.3	-	-	0.3	-	0.3
<i>Thesium alpinum</i> L.		Other spp.	0.3	2.2	-	-	-	-
<i>Thymus pulegioides</i> L.		Other spp.	1.6	3.4	-	-	-	-
<i>Trifolium alpinum</i> L.		Legumes	-	-	-	0.3	-	-
<i>Trifolium aureum</i> Pollich		Legumes	0.3	-	-	-	-	-
<i>Trifolium badium</i> Schreb.		Legumes	5.2	6.7	4.0	-	-	0.3
<i>Trifolium montanum</i> L.		Legumes	2.2	-	-	-	-	-

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<i>Trifolium pallescens</i> Schreb.	Tri.pall	Legumes	0.7	-	-	-	-	12.1
<i>Trifolium pratense</i> L.	Tri.prat	Legumes	4.8	19.8	2.0	-	6.5	1.4
<i>Trifolium repens</i> L.	Tri.repe	Legumes	1.9	4.9	16.6	-	-	-
<i>Trisetaria distichophylla</i> (Vill.) Paunero	Tri.flav	Broadleaf grasses	-	-	-	-	-	2.2
<i>Trisetaria flavescens</i> (L.) Baumg.		Broadleaf grasses	1.5	22.7	11.9	-	-	-
<i>Valeriana celtica</i> L.		Other spp.	-	-	-	0.3	-	-
<i>Veratrum album</i> L.		Other spp.	-	0.3	-	-	-	-
<i>Veronica bellidioides</i> L.		Other spp.	-	-	-	2.2	-	0.3
<i>Veronica chamaedrys</i> L.		Other spp.	-	3.7	0.3	-	-	-
<i>Veronica fruticans</i> Jacq.		Other spp.	3.9	-	-	-	-	-
<i>Veronica serpyllifolia</i> L.		Other spp.	-	0.3	0.3	0.5	1.7	0.7
<i>Viola calcarata</i> L.		Other spp.	2.8	4.0	0.3	-	-	-
<i>Viola</i> sp.		Other spp.	4.0	0.3	-	-	-	-

Bartolucci F., Peruzzi L., Galasso G. et al., 2018. An updated checklist of the vascular flora native to Italy. *Plant Biosyst- Int J Deal Asp Plant Biol*, 152, 179–303.

5. Overall considerations and perspectives

The results gathered from the present thesis confirm the remarkable role played by alpine vegetation communities in providing a whole range of ES. The specific insights addressed in the different chapters help to fill in some knowledge gaps. We observed that vegetation dynamics were rapid in proglacial environment even at very high altitudes (chapter 2). Despite the relatively low cover, vegetation triggered pedogenetic processes and their magnitude depending on the different plant species. Late-successional species produced more intense effects than pioneer plants, but likely require soil previously developed by these latter for their establishment. The dynamics of organic C, N and P were strongly influenced by colonising plants. Further, we observed that, along a proglacial chronosequence in which the intensity of natural disturbances (i.e., rock falls, water erosion, etc.) is limited, autogenic and deterministic processes of the primary succession can be relevant. The retreat of glaciers caused by ongoing climate change will release large new unstable rocky slopes in the coming decades. The implementation of permanent observatories on soil-vegetation dynamics in such a critical ecosystem will help to improve the current knowledge on the ecology of these environments and of the provision of specific ES, while allowing to identify the trajectories that alpine ecosystems and landscapes will likely experience.

Adverse climate change will inevitably impact the dynamics of soil C stocks in mountain ecosystems and thus also in alpine grasslands. Our results obtained on a large sample of alpine grasslands in the Western Alps (chapter 3) showed an important accumulation of organic C in soils underlying thermophilic and xeric vegetations. The expected climatic scenarios for the Western Alps envisage an intensification of summer droughts, with an increase in the frequency of heat waves and a change in the distribution of precipitation, probably more concentrated in winter and spring than in summer. These phenomena could perhaps partially offset the negative effects that will occur on other plant communities, such as those more dependent on water availability like mountain wetlands. Additionally, the pastoral practices that would be implemented at a local scale should aim at preserving thermophilic and xeric pastoral types from shrub and tree encroachment which is one of the major threats to such grasslands.

The production and quality of forage, one of the most important resources produced by alpine plant communities, are considerably sensitive to water availability and temperatures (Chapter 4) and climate worsening will likely affect them with a remarkable importance. Our

results provide some early suggestions for suitable pastoral management through increasing the cover of specific pool of plants to counteract the effects of climatic stress on forage yield and proximate composition. Implementing optimal grazing strategies with balanced stocking rates would improve soil fertility by means of livestock dung and urine depositions, encouraging an increase in the cover of broadleaf grasses, which are able to provide abundant, rich in sugars and highly digestible forage.

Future research should proceed to investigate the ecological interactions between alpine plant ecosystems and their role in the provision of ES. The economic evaluation of ES delivered by mountain agro-ecosystems can provide new opportunities for the development of rural regions. Payment for Ecosystem Services (PES) is a highly topical issue in the context of the so-called green economy, in terms of new jobs, new products, new markets, and new values. The development of PES in rural and mountain areas, based on the findings achieved through ecological research, can increase their attractiveness and help to halt the current demographic decline, a phenomenon at the root of many socio-economic and environmental issues in mountain areas in the current era.

General Appendix

Annex A

Dinamiche ed effetti pedogenetici delle specie erbacee pioniere e definitive lungo una cronosequenza glaciale delle Alpi occidentali (Parco Nazionale Gran Paradiso)

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Abstract

A partire dalla fine della piccola età glaciale, le coltri glaciali dell’Artide e delle Alpi hanno subito generalmente forti contrazioni, esponendo superfici via via sempre più vaste alla pedogenesi e alla colonizzazione vegetale. L’approccio comunemente più utilizzato per lo studio delle successioni primarie in ambiente periglaciale prevede la definizione di una cronosequenza, intesa come serie consecutiva di superfici deglacializzate da periodi differenti e noti. Negli ultimi 50 anni, ecologi e pedologi si sono occupati di molteplici aspetti legati alle dinamiche della vegetazione, del suolo e delle interazioni tra i due comparti del sistema lungo varie cronosequenze glaciali. L’effetto delle specie arboree, arbustive ed erbacee sulle proprietà chimiche e lo sviluppo del suolo è stato altresì approfondito in numerosi contesti ambientali. Tuttavia, l’impatto di specie erbacee riconducibili a stadi differenti della successione (ossia, pioniere e definitive) sulla biogeochimica del suolo in una successione primaria risulta tuttora poco noto. L’obiettivo del lavoro è valutare l’interdipendente dinamica del sistema suolo-pianta lungo una cronosequenza glaciale, evidenziando modificazioni ecosistemiche stocastiche/deterministiche operate da specie pioniere e

definitive. Lo studio è stato condotto sul detrito morenico del ghiacciaio del Lauson nel Parco Nazionale Gran Paradiso (Cogne, AO) dove è stato possibile identificare e datare sei differenti stadi della cronosequenza, distribuiti in un arco temporale di circa 170 anni. La vegetazione è stata rilevata su 18 plot permanenti (tre per stadio) tramite metodo fitosociologico. In seguito, sono stati calcolati la copertura vegetale delle piante vascolari e delle crittogame, gli indici di diversità specifica e il numero di specie e la copertura di due differenti gruppi funzionali: il gruppo delle specie pioniere (riconducibili a *Thlaspietea rotundifolii*) e quello delle specie tipiche di prateria alpina (riconducibili a *Caricetea curvulae*). Parallelamente è stato condotto un approfondimento specifico sulla struttura dei popolamenti di due specie obiettivo: *Saxifraga oppositifolia* L. subsp. *glandulifera* Vacc., specie spiccatamente pioniera, e *Silene acaulis* (L.) Jacq. subsp. *bryoides* (Jord.) Nyman, specie marcatamente più esigente. Per ciascun individuo presente nei plot sono stati rilevati due diametri perpendicolari e la relativa media è stata assunta come indicatore dell'età. In corrispondenza di ciascun stadio della cronosequenza è stato aperto un profilo pedologico e sono stati prelevati i campioni di ogni orizzonte individuato per la caratterizzazione chimica. Per valutare l'influenza delle specie obiettivo sul chimismo e l'evoluzione del suolo, sono stati prelevati, in ogni stadio della cronosequenza, campioni di suolo sotto gli individui delle due specie e in aree prive di vegetazione. Infine, le stesse piante eradicate per la raccolta dei suoli sono state campionate per le analisi chimiche in laboratorio dei tessuti fotosintetici.

Il numero e la copertura delle specie pioniere raggiungono i valori massimi rispettivamente dopo 10 e 40 anni dalla deglaciazione, mentre il numero e la copertura delle specie tipiche di prateria alpina raggiungono il loro massimo a 140 e 65 anni dal ritiro del ghiacciaio. Lungo la cronosequenza, il suolo sottostante gli individui di *S. oppositifolia* e *S. acaulis* risulta maggiormente arricchito in nutrienti rispetto ai suoli delle aree prive di copertura vegetale. *S. acaulis*, specie a pulvino compatto, esercita un'influenza più importante rispetto a *S. oppositifolia* (specie a portamento prostrato e lasso) e contribuisce ad accumulare da 1.3 a 8.9 g kg⁻¹ di C nel suolo (da 0.2 a 3.3 g kg⁻¹ nelle aree prive di copertura vegetale). L'azoto presenta concentrazioni sotto le soglie di rilevabilità nei suoli privi di copertura vegetale, mentre aumenta nei suoli sotto le piante e con il tempo dalla deglaciazione, equilibrando i rapporti stechiometrici C:N:P dei suoli più sviluppati verso valori favorevoli per l'affermarsi della vegetazione.

Complessivamente lungo la cronosequenza glaciale del Lauson è stata

rilevata una colonizzazione precoce e ricca in specie nei micro-siti favorevoli per l'insediamento. L'effetto dovuto dall'insediamento delle specie erbacee pioniere stimola lo sviluppo del substrato, pressoché inerte nelle primissime fasi dalla deglaciazione, predisponendo la successiva colonizzazione delle specie più competitive di prateria. Le specie tipiche della prateria alpina attecchiscono sporadicamente già nelle prime fasi post-glaciali, tuttavia incrementano significativamente in termini di numerosità e copertura solamente dopo che il suolo ha acquisito un'iniziale funzionalità. Tali evidenze supportano un determinismo biotico della successione primaria, riscontrabile già nelle prime fasi post-glaciali. Tuttavia, dopo circa 170 anni la copertura vegetale si attesta intorno al 30%, ancora lontana (anche in termini di composizione) dalla comunità climax del curvuleto, pertanto non raggiunta. L'ecosistema permane inoltre C-N-limitato mentre il P appare il macroelemento maggiormente a disposizione per la crescita vegetale.

Annex B

Confronto tra Metodo Fitopastorale e Metodo Fitosociologico per il calcolo del Valore Pastorale in praterie xeriche delle Alpi Occidentali

An edited version of this oral contribution has been published in the book of abstract of the “115° Congresso della Società Botanica Italiana” (ISBN 978-88-85915-24-4), online, 9-11 September 2020 and it is here reproduced with permission from the authors:

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Abstract

Il valore pastorale (VP) è un indice ricavato dalla composizione botanica di un pascolo che sintetizza le caratteristiche produttive, qualitative e pabulari della vegetazione come foraggio per il bestiame. Il VP è largamente utilizzato nella gestione pastorale delle praterie per determinare la capacità di carico. Il metodo classico di rilievo impiegato per il calcolo del VP è quello fitopastorale, proposto da Daget et Poissonet. Questo metodo restituisce una stima accurata dell'abbondanza delle specie vegetali dominanti, ma tende a sottostimare la ricchezza specifica in quanto le specie occasionali spesso non sono rilevate. Dall'altra parte, il metodo fitosociologico proposto da Braun-Blanquet consente di determinare in maniera più esatta la composizione floristica, ma la sua applicazione per il calcolo del VP è stata scarsamente valutata. L'obiettivo di questo lavoro è quello di valutare l'adeguatezza del metodo fitosociologico per il calcolo del VP, rispetto al metodo classico fitopastorale, nelle praterie xeriche delle Alpi Occidentali. Questo lavoro rappresenta il primo studio comparativo dei due metodi realizzato in ambiente alpino.

Lo studio è stato condotto in praterie appartenenti alla classe *Festuco-*

Brometea, nelle Alpi Occidentali piemontesi (45°08'N, 7°06'E, ZSC IT1110030). Nel 2014 sono stati realizzati 140 rilievi vegetazionali utilizzando sia il metodo fitopastorale, sia quello fitosociologico. La prima metodologia è stata applicata su transetti di 12.5 m, con 50 calate, mentre la seconda è stata applicata in plot di 2 x 12.5 m centrati sui transetti. Per entrambi i metodi è stata calcolata l'abbondanza relativa (%) di ciascuna specie vegetale, da cui è stato ricavato il VP secondo la formula proposta da Daget et Poissonet. La corrispondenza fra i due metodi di rilievo nella stima della ricchezza specifica e del VP è stata valutata con una regressione lineare. Inoltre, i VP ottenuti a partire dalle due metodologie sono stati confrontati a livello di tipo pastorale, mediante t-test appaiati. I tipi pastorali sono stati individuati tramite cluster analysis (metodo, UPGMA; indice di similarità, Pearson).

Il metodo fitosociologico ha restituito valori di ricchezza specifica più elevati rispetto a quello fitopastorale (Fig. B.1 a), mentre il VP è risultato molto simile fra i due metodi (Fig. B.1 b). Non sono state osservate differenze significative fra i VP calcolati a partire dai due metodi per nessuno dei tipi pastorali individuati (tipo a *Festuca ovina* s.l., tipo a *Brachypodium rupestre*, tipo a *Stipa pennata* s.l. e tipo a *Chrysopogon gryllus*), eccetto che per il tipo a *Bromus erectus* (VPfitop = 20.5 ± 0.62 , VPfitos = 17.6 ± 0.65 ; $P < 0.001$).

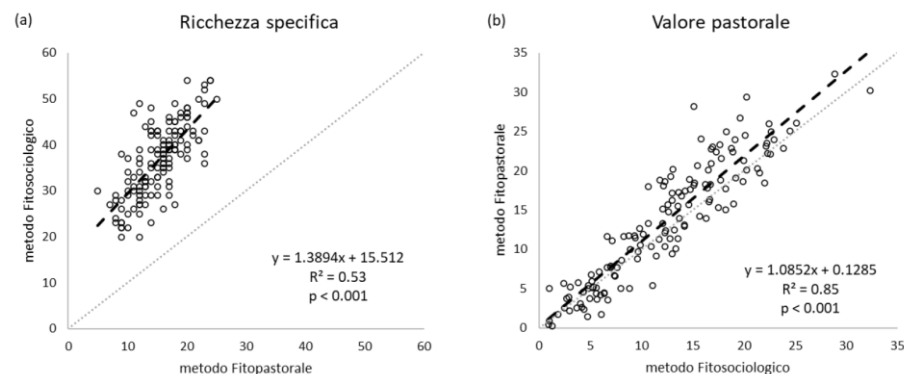


Figura B.1. Regressione lineare realizzata per (a) la ricchezza specifica e (b) il Valore pastorale calcolati a partire dal metodo fitopastorale e fitosociologico.

I risultati dimostrano l'efficacia del metodo fitosociologico nel calcolo del VP per la maggior parte dei tipi pastorali di praterie xeriche esaminati. L'accuratezza della stima visiva delle coperture mediante metodo fitosociologico potrebbe esser stata facilitata dalla struttura tipica di queste comunità vegetali, caratterizzate da vegetazione di piccola taglia e da una considerevole quantità di suolo nudo. Tuttavia, per il tipo a *Bromus erectus*, il metodo fitosociologico ha restituito VP più bassi,

probabilmente perché l'abbondanza della specie dominante è stata sottostimata (in media, 28%) rispetto al metodo fitopastorale (39%). Sarebbe certamente di grande interesse la realizzazione di studi comparativi analoghi anche in altri tipi pastorali, come in quelli più produttivi e di condizioni mesofile.

Annex C

Relative importance of topography, climate, species composition, and phenology in affecting forage yield and quality in alpine summer pastures

An edited version of this oral contribution has been published in the book of abstract of the “1st Joint Meeting of EAAP Mountain Livestock Farming & FAO-CIHEAM Mountain Pastures – Mountains are agroecosystems for people”, Bled (Slovenia), online, 7-9 June 2021, p. 110 and it is here reproduced with permission from the authors:

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Abstract

Keywords: pasture, proximate composition, digestibility, forage productivity, biomass

Introduction: High quality and healthy food demands have continuously increased in Europe over the last years. Grasslands play a crucial role in providing milk, meat and other edible products in large areas around the world. The extensive long permanent grasslands hold a high plant species diversity and often support the provision of valuable forage sources. Particularly, the forage produced by mountain summer pastures is generally the only feed for grazing livestock. The main issue in alpine pasture management is the optimal exploitation of the available forage resource in relation to seasonal advancement, altitude and vegetation composition. However, little is still known about forage yield of species-rich alpine pastures and related chemical composition. In this work, we aim at characterizing forage quantity and quality (i.e., digestibility and proximate composition) exploring the relationships with topographic, climatic and vegetation variables along the growing season. We focused on six grassland types in the western Italian Alps,

characterized by contrasting environmental conditions and vegetation compositions.

Materials and methods: The study was carried out in an alpine valley of the Gran Paradiso National Park, in the south-western Italian Alps. We selected six grassland types within two altitudinal (lower: 2300 m a.s.l.; higher: 2750 m a.s.l.) and three fertility (oligotrophic, mesotrophic and eutrophic) levels. Each grassland type was surveyed five times (three replicates) during summer 2019 and 2020, for a total of 162 vegetation surveys. Once plant species composition was assessed, the relative percentage covers of different functional species pools (i.e., broadleaf grasses, narrow-leaved grasses, sedges and rushes, legumes, other species) were computed. A grass sample was harvested at each survey using a portable lawn-mower (cutting height 1 cm), then air-dried, weighed and analysed with near infrared reflectance spectroscopy (NIRS) technique for proximate composition and digestibility. Topographic variables (i.e., elevation, slope) were recorded in the field. Temperatures and precipitations were measured throughout the trial and combined in a synthetic eco-climatic variable (ΔPrET) calculated as the difference between the total precipitation and the potential evapotranspiration (according to the Hargreaves equation) from the day of snowmelt. Plant phenology as well was recorded according to the Lambertin scale. Data were analysed with Generalized Linear Mixed Models to assess the relative importance of topographic (altitude, slope and southness) and climatic (ΔPrET and mean temperatures between surveying period) variables, plant phenology and functional species pool covers in explaining forage yield and quality (in terms of digestibility, crude protein, NDF, ADF, ADL, soluble sugars).

Results: Herbage quality (except for soluble carbohydrates) was negatively affected by ΔPrET , with a larger relative importance compared to the other explanatory variables (digestibility: ΔPrET $\beta = 0.18$, $p < 0.001$; Phenology $\beta = -0.11$, $p < 0.001$; sedges and rushes $\beta = -0.04$, $p < 0.01$). Plant phenology showed a remarkable role in explaining also crude protein and fibre contents (i.e., NDF, ADF, and ADL). More specifically, a decrease in crude protein and an increase in fibre fractions was observed at advanced phenophases, thus resulting in a reduced digestibility. The cover of broadleaf 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 increasing cover of sedges and rushes and mean temperatures, respectively (biomass: elevation $\beta = -0.58$, $p < 0.001$; broadleaf grasses $\beta = 0.42$, $p < 0.001$; slope $\beta = -0.38$, $p < 0.05$; sedges

and rushes $\beta = 0.18$, $p < 0.001$; mean temperatures $\beta = 0.15$, $p < 0.01$). At increasing cover of legumes, NDF declined and digestibility increased consequently.

Conclusion: Eco-climatic variables as water stress (i.e., ΔPrET) and phenology were the main degrading factors of forage quality in the study area. Nevertheless, the abundance of high-quality forage species (i.e., broadleaf grasses and legumes) can counterbalance these negative processes. Pastoral management in the alpine environment should therefore aim to maintain and enhance these functional species pools, especially to face the ever more frequent summer droughts and heat waves.

Annex D

Relative importance of topography, climate, species composition, and phenology in affecting forage yield and quality in alpine summer pastures

An edited version of this oral contribution has been published in the book of abstract of the “1st Joint Meeting of EAAP Mountain Livestock Farming & FAO-CIHEAM Mountain Pastures – Mountains are agroecosystems for people”, Bled (Slovenia), online, 7-9 June 2021, p. 110 and it is here reproduced with permission from the authors:

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Abstract

Keywords: grassland, elevation, precipitation, slope, pH

Introduction: The role of land uses able to counteract current climate change, namely efficiency in carbon stocking, is becoming essential worldwide. Mountain pastures can provide many ecosystem services, such as provisioning services (e.g. biodiversity, forage), regulation and maintenance services (e.g. water purification, soil retention), and cultural services (e.g. nature-based recreation, eco-tourism) as well as relevant soil C stocks. However, little is known about the variability of soil C stock in Alpine pastures according to different climatic, environmental, and vegetational features. The present study aimed at evaluating the relative

importance of various abiotic and biotic drivers in affecting soil C stock in a wide sample of Alpine pastures.

Materials and methods: Between 2000 and 2007, we carried out 324 surveys encompassing a wide geographical and ecological range across the Western Italian Alps, including 54 different vegetation types. At each site, the complete botanical composition of grassland vegetation was determined through the vegetation point-quadrat method, along 25-m transects. At each transect, the relative abundance of every species was calculated as the proportion of the frequency of occurrence of each species. Species relative abundances were used to perform a non-metric multidimensional scaling (NMDS) to take the vegetation composition of each survey into account in further analyses. Additionally, a soil sample in the 0-30 cm layers was collected close to every vegetation transect and analysed for pH and organic C content (following the Walkley-Black procedure). Furthermore, bulk density was estimated according to the CREA-AA methods and used for the assessment of C stock. Mean annual precipitation (1977-2007 data series), elevation, slope, and southness were computed for each survey point and included, together with pH and the three main components of the NMDS, in a generalized linear model to predict C stock. Gaussian family was applied and the identity function was specified. Statistical analyses were carried out in R environment, using 'vegan' and 'glmmTMB' packages.

Results: Plant species distribution in the NMDS displayed a thermic-altitudinal positive gradient on the first axis, a biomass productivity negative gradient on the second axis, and a soil nutrient positive gradient on the third axis. Soil C stock of the investigated pastures varied between 1.9 and 234.9 t ha⁻¹, with an average value of 87.8 (standard error: 2.09) t ha⁻¹. According to glm results (Table D.1), C stocks were significantly influenced by mean annual precipitation, soil pH, and the first axis of NMDS. Elevation, slope and southness showed non-significant effects as well as the second and third NMDS axes.

Conclusion: The novel results of this study highlighted the relevant importance of grassland species composition in affecting soil C stock in Alpine environment, while topographic attributes had negligible effects. More specifically, dry pastures on calcareous bedrock (which also

generally host rare plants and a high species richness) stocked more Carbon in the soil. Future conservation strategies should aim to consider the role of dry grassland species in enhancing this ecosystem service. Nonetheless, more detailed research concerning the effects of pastoral management practices on C stock of Alpine pastures appears still required.

	β scores	SE	p	
Precipitation	9.994	2.515	<0.001	***
Elevation	7.619	4.206	0.070	
Slope	0.241	2.325	0.917	
Southness	0.182	2.237	0.935	
Soil pH	-8.574	2.752	0.002	**
NMDS1	-11.782	4.068	0.004	**
NMDS2	-3.611	2.897	0.213	
NMDS3	-1.991	2.218	0.369	

Table D.1. Relative importance of explanatory variables in affecting C stocks of Alpine pastures, according to generalised linear model results. SE, standard errors; p, p values; NMDS, non-metric multidimensional scaling.

Annex E

Other publications and participation to congresses
Full papers on ISI journals

- Galasso G., Domina G., Ardenghi N. M. G., Aristarchi C., Bacchetta G., Bartolucci F., ... Mainetti A., ... Nepi C., 2019. Notulae to the Italian alien vascular flora: 7. *Italian Botanist*, 7, 157–182.
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Poster at international congresses

The BambApp project: a citizen science network for monitoring and defining the distribution of bamboos in piedmont and aosta valley (NW-Italy)

Poster presented at the VI International Plant Science Conference (IPSC)-114° Congresso della Società Botanica Italiana. Padova (Italy), 4–7 September 2019

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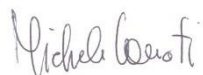
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