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Bertrand Dumont, Donato Andueza, Vincent Niderkorn, Andreas Lüscher,
Claudio Porqueddu, Catherine Picon-Cochard

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Abstract: Atmospheric CO₂, global mean temperature and inter-annual variability in temperature and rainfall are expected to be significantly higher by the end of the 21st century. In order to review the effects of these factors on forage quality, we carried out a meta-analysis based on climate manipulation experiments. The outputs are reported in this deliverable.

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Authors: [B. Dumont \(INRA\)](#), [D. Andueza \(INRA\)](#), [V. Niderkorn \(INRA\)](#), [A. Lüscher \(WBF Agroscope\)](#), [C. Porqueddu \(CNR-ISPAAM\)](#), [C. Picon-Cochard \(INRA\)](#)

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A meta-analysis of climate change effects on forage quality in grasslands: perspectives for mountain and Mediterranean areas

Abstract. Atmospheric carbon dioxide (CO₂), global mean temperature and inter-annual variability in temperature and rainfall are expected to be significantly higher by the end of the 21st century. In order to review the effects of these factors on forage quality, we carried out a meta-analysis based on climate manipulation experiments. A first original output is the absence of effect of elevated CO₂ on structural carbohydrates (NDF, ADF, lignin), and digestibility. Elevated CO₂ decreased by an average of 9% forage nitrogen (N) content, but the concentration of N in the harvested biomass could be maintained as the result of increased legume abundance. There were no consistent effects of warming on N, water-soluble carbohydrates, NDF, ADF and digestibility. We highlighted the continuum in the effect of water availability from drought to irrigation, with a curvilinear increase of forage N response as water availability decreased. Digestibility increased on average by 10% with drought, but with strong experimental variations. Special emphasis is placed on the discussion of the specificities of mountain and Mediterranean grasslands. Forage N content increased by an average of 9% as a response to warming in mountain areas compared with a 2% decrease in temperate plains. In Mediterranean areas, forage N content was only reduced by 1% as the result of elevated CO₂. In conclusion, we did not observe any dramatic change in forage quality induced by each climate change factor, but further experiments should test for the effects of combined factors including extreme climatic events.

Keywords. Elevated CO₂ – Warming – Precipitation change – Nitrogen – Non-structural carbohydrates – Fibres – Digestibility

Introduction

Global atmospheric change consists of i) an increase of the main greenhouse gases: CO₂, methane and nitrous oxide and ii) transient changes in temperature, precipitation and other climatic elements over the next decades to centuries. For the preparation of the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2013a) global projections of the earth's climate have been developed using general circulation models for a set of new emission scenarios, the so called Representative Concentration Pathways (RCPs). The latter are referred to as concentration pathways in order to emphasize that they are not definitive socioeconomic scenarios, but rather internally consistent sets of time-dependent projections of climate forcing that could potentially be realized with more than one underlying socioeconomic scenario (Collins *et al.*, 2013).

The increase in atmospheric CO₂ concentration is the most reliable aspect of global atmospheric change. The increase of atmospheric CO₂ concentration has been from 338 ppm to 398 ppm between 1980 and 2014. According to the four widely varying RCPs, atmospheric CO₂ concentration by 2100 could reach 421 ppm (RCP2.6, low), 538 (RCP4.5, medium-low), 670 ppm (RCP6.0, medium-high) or 936 (RCP8.5, high) (IPCC, 2013b). With respect to RCP4.5 and taking the scenario uncertainty into account, the earth's annual mean surface air temperature is expected to increase relative to 1986–2005 by +1.1 to +2.6°C (Collins *et al.*, 2013). Maximum warming is expected to occur in the high latitudes of the northern hemisphere. In Europe, warming is projected to be strongest in the Northwest (NW), where it may reach +3 to +7°C in winter, while the hotspot for warming in summer is projected in the Iberian Peninsula with +3 to +4°C (IPCC, 2013c). Lelièvre *et al.* (2010) reported that in southern France the boundaries of Mediterranean climate moved to the North and NW at the rate of 30-40 km per decade since 1980. In winter, however, temperature increase in the Mediterranean region is projected to be relatively mild (+1 to +2°C) by the majority of models. Increased inter-annual variability may be another significant aspect of climate change, and this is of high ecological relevance. Using a regional climate model, Schär *et al.* (2004) predict for central Europe that year-to-year temperature variability will increase by up to 100% by 2071-2100. This would lead

to more frequent heat waves and droughts during the growing season. All climate models suggest that average precipitation will increase although reductions are likely in some regions. For 2100 and the RCP4.5 an increase in precipitation by +10 to +20% both in winter and summer is projected for Northern Europe (IPCC, 2013c). For the Mediterranean region a slight reduction of precipitation of 0 to -10% in winter and -10 to -20% in summer is projected. The magnitude of regional precipitation change varies considerably amongst models, and in many areas is less than the standard deviation of model-estimated natural variability.

The objective of this paper is to review the current knowledge on the effects of the impact of atmospheric change – elevated CO₂, increased temperature, and drought – on a wide range of forage quality parameters. The basis of this review is a meta-analysis based on climate manipulation experiments covering a wide range of climatic conditions and all types of grasslands (permanent grasslands, temporary grasslands, mixtures). Special emphasis is placed on the discussion of the specificities of mountain and Mediterranean grasslands.

I - Impact of climate change on plant ecophysiology and livestock digestion

Forage quality depends on nutrient concentration, which determines digestibility, partitioning of metabolized products in the digestive tract and forage intake; it thus strongly affects animal performance. Forage quality is estimated by chemical or biological analyses. Chemical analyses include ash and nitrogen (N) content, total non-structural carbohydrate content (water soluble carbohydrates: WSC and starch), and structural fibres (neutral detergent fibre: NDF, acid detergent fibre: ADF, lignin: ADL). Biological analyses are mainly based on the estimation of the dry matter digestibility either using ruminal fluid *in vitro* (Telly and Terry, 1963) or enzymes (Aufrère and Demarquilly, 1989).

Climate change impacts livestock digestion in two ways, i) its effects on the physical and chemical characteristics of forages, and ii) its direct effects on digestive processes. Ecophysiological changes in plants in response to a heat stress depend on warming level and drought intensity. Extreme climatic events lead to tissue senescence that strongly decrease forage quality. Under moderate heat stress, plant maturation is faster, water content of plant tissues decreases while WSC increase. Maturation of plants increases stem-to-leaf ratio and cell wall content, including lignin which interferes with the digestion of cell wall polysaccharides by acting as a physical barrier to microbial enzymes (Moore and Jung, 2001). High temperatures amplify the lignification process by increasing cell lignification rather than the proportion of cells becoming lignified (Wilson *et al.*, 1991). Consequently, heat stress usually decreases DM digestibility (Lu, 1989). However, under elevated CO₂, an increase of WSC content and a corresponding decline in cell wall content can increase DM digestibility (Picon-Cochard *et al.*, 2004), which reveals complex interactions between climatic factors.

It has been well documented that high temperatures decrease voluntary intake by ruminants due to thermoregulation since most of heat production is due to rumen fermentations (Beatty *et al.*, 2008). O'Brien *et al.* (2010) showed that heat stress consequently reduced the performance of growing cattle. Animals can adapt their foraging behaviour, e.g. reduce feeding bout duration, and increase night feeding. In addition, increasing nutrient density (because dietary protein degradability may become critical), and limiting high-fibre diets (to decrease heat production) can help maintaining normal rumen function (West, 2003). Some direct impacts of heat stress on digestion have also been reported such as a slower passage rate and a longer retention time of digesta in the gastrointestinal tract (Silanikove, 1992). Slower passage rates may partly result from changes in reticular motility (Miaron and Christopherson, 1992). Reduced daily intake, associated with a decrease in volatile fatty acid concentration in the rumen and prolonged retention of feed in the gastrointestinal tract, could increase forage digestibility (Schneider *et al.*, 1988; Miaron and Christopherson, 1992). Bernabucci *et al.* (2009) recently revealed that variations of diet digestibility in ewes chronically exposed to heat stress could also result from adaptation of rumen function to hot environments with less cellulolytic and amylolytic bacteria.

II - A meta-analysis based on climate manipulation experiments

For conducting the meta-analysis, we created a database (references in Table 1) of climate change effect (elevated atmospheric CO₂ concentration, warming, drought or irrigation, and their interactions) on forage quality variables using the Web of Science in November 2013. Search terms were 'climate change' and 'forage quality' or 'nitrogen' or 'carbohydrate' or 'fibre' or 'phosphorus' or 'nutrients' or 'lignin' or 'digestibility' or 'NDF' or 'ADF' or 'ADL'. A total of 81 papers were selected, but only 50 were used after excluding reviews and original papers with unavailable data (e.g. ANOVA results were given rather than mean values) or infrequent quality variable (e.g. tannins, macro-nutrients that were analyzed in less than six papers). Additional 21 papers were used to complete the database, based on a second round of search with terms 'warming' or 'drought' or 'water deficit' or 'water stress' and 'forage' or 'grassland' and 'nutritive value' or 'chemical composition' or 'digestibility'. A total of 71 papers were thus finally analyzed. Short-term climate manipulation experiments apply single or combined climate change factors in a controlled way and thus allow testing scenarios. Outdoor experiments with natural ecosystem were preferred, but some experiments performed in semi-controlled conditions were also selected. We included some data on shrubs and tree foliage since they are occasionally browsed especially in Mediterranean areas, and an altitudinal gradient experiment (Xu *et al.*, 2002). Atmospheric CO₂ concentration was increased on average by 283 ± 102 ppm (mean ± SD, n = 340 observations from 41 experiments in the database) compared with ambient CO₂ 366 ± 20 ppm; air or canopy temperature was increased by an average of 3.7 ± 4.6 °C (n = 205 observations, 25 experiments) during the growing season compared with ambient temperature 12.3 ± 5.4 °C, which broadly corresponds to the medium-high RCP scenario (IPCC, 2013b). Precipitation were reduced by 49 ± 34 % in drought experiments (n = 83 observations, 14 experiments) and water supply was increased by 78 ± 68 % in irrigation trials (n = 111 observations, 9 experiments). Few experiments combined several factors (n = 113 observations, 12 experiments). The effect of climate change was sometimes analyzed according to season, N fertilization, and grazing or defoliation regimes. Forage quality was measured on organs (leaf lamina, sheaths and stems), plant species, mixtures or plant communities. Species were therefore grouped according to functional group: C₃ grasses (GC₃), C₄ grasses (GC₄), Legumes (L), Forbs: non N-fixing dicots (F), *Cyperaceae* (C), or woody (shrubs).

Table 1. Main characteristics of climate manipulation experiments used in the meta-analysis.

Ecosystem †	Vegetation type	Quality variables	Treatments	Ref.
Semi-arid plains				
Native rangeland	GC ₃ , GC ₄ , F	N	CO ₂	[1]
Mixed-grass prairie	GC ₃ , GC ₄	N	CO ₂ , T	[2]
Mixed-grass prairie	GC ₃ , GC ₄	N/P	CO ₂ , T	[3]
Shortgrass steppe	G, F, Sedges	N	D	[4]
Subtropical plains				
Tallgrass prairie	GC ₃ , GC ₄ , F	N, C/N	T	[5]
<i>Phalaris aquatic</i> , <i>Trifolium subterraneum</i> †	GC ₃ , L	N, Dig, TNC	CO ₂ , T	[6]
<i>Arachis glabrata</i> †	L	NDF, ADF, ADL, Dig	CO ₂ , T	[7]
<i>Holcus lanatus</i> , <i>Pennisetum clandestinum</i>	GC ₃ , GC ₄	N, C/N, ADL	CO ₂	[8]
Tallgrass prairie	GC ₃ , F	N	T	[9]
Temperate plains				
<i>Deschampsia flexuosa</i>	GC ₃	C/N	CO ₂ , T, D	[10]
Temperate grassland	GC ₃ , GC ₄ , F, L	N, NDF, ADF, WSC, Dig	CO ₂	[11]
<i>Phleum pratense</i> ‡	GC ₃	N, P, WSC, starch, TNC, NDF, ADF, ADL, Dig	T	[12]
<i>Lolium arundinaceum</i>	GC ₃	N, C/N, NDF, ADL	CO ₂ , D, T	[13]
<i>Cichorium intybus</i> ,	F, L	N	D	[14]

<i>M. sativa, T. pratense</i>	GC ₃ , F	N	CO ₂	[15]
Grassland species	GC ₃	N	CO ₂	[16]
<i>Lolium perenne</i>	GC ₃	N	CO ₂	[17]
<i>Medicago sativa</i>	L	TNC, NDF, ADF, ADL, Dig	D	[18]
<i>Lolium perenne</i>	GC ₃	WSC	CO ₂	[19]
<i>Trifolium repens</i>	L	N, Dig	CO ₂	[20]
<i>Medicago sativa</i>	L	N, NDF, ADL, Dig	D, W	[21]
<i>Lolium perenne</i>	GC ₃	Starch, TNC	CO ₂	[22]
Grassland species	GC ₃ , GC ₄ , F, L	N, ADL	CO ₂	[23]
Semi-natural heathland	GC ₃ , F	C/N	CO ₂ , T, D, and all interactions	[24]
<i>Festuca arundinacea</i>	GC ₃	N, ADL	CO ₂	[25]
Temperate grassland	GC ₃ , GC ₄ , F, L	N	CO ₂	[26]
<i>Phleum pratense</i> ‡	GC ₃	WSC, starch	CO ₂ , T	[27]
<i>Pascopyrum smithii</i> , <i>Bouteloua gracilis</i> †	GC ₃ , GC ₄	N, TNC	CO ₂ , T, CO ₂ xT	[28]
<i>Plantago lanceolata</i> , <i>T. officinale</i> , <i>E. repens</i> †	GC ₃ , F	N, C/N	T	[29]
<i>Trifolium ambiguum</i> , <i>M. sativa</i> , <i>T. pratense</i>	L	N, NDF, ADL, Dig	W	[30]
Perennial grass species	GC ₃	N, NDF, ADL	W	[31]
Legume species	L	N, NDF, ADF	W	[32]
Grass and legume species	GC ₃ , L, F	N, NDF, Dig	D	[33]
Grass species †	GC ₃	N	CO ₂	[34]
<i>Alopecurus pratensis</i>	GC ₃	N, C/N	D	[35]
<i>Holcus lanatus</i>	GC ₃	N, C/N, WSC	D	[36]
<i>Lolium perenne</i>	GC ₃	N	CO ₂	[37]
Sub-arctic/arctic climate				
Bog species	GC ₃ , F	N, P	T	[38]
Semiarid steppe	GC ₃	N	W	[39]
Deciduous dwarf shrubs	Woody	N	T	[40]
<i>T. pratense</i> , <i>T. repens</i>	L	N, NDF, ADL, Dig	CO ₂	[41]
Tundra	Cyp	N	T, W	[42]
Tundra	Cyp	N, C/N	T	[43]
Mountain climate				
<i>Agrostis capillaris</i> , <i>Festuca viviparia</i> , <i>Poa alpina</i>	GC ₃	N, P	CO ₂	[44]
<i>A. capillaris</i> , <i>F. vivip.</i> , <i>P. alpina</i>	GC ₃	WSC, starch, TNC	CO ₂	[45]
<i>Festuca paniculata</i>	GC ₃ , F, L	N, WSC	TxD	[46]
Perennial grassland	GC ₃ , GC ₄	N	T, TxD, TxDxCO ₂	[47]
Mixed grass prairie	GC ₃ , F	N	CO ₂ , T	[48]
Glacier forefield species	GC ₃ , F	N, C/N, WSC	CO ₂	[49]
<i>D. glomerata</i> , <i>L. perenne</i>	GC ₃	N, NDF, Dig	W	[50]
Perennial grassland species	GC ₃	N, NDF, Dig	W	[51]
Shortgrass steppe	GC ₃ , GC ₄	N	CO ₂	[52]
Meadow and shrubland	F, Sedges	N	T	[53]
Perennial grassland species	F, L, Cyp	N, WSC	CO ₂	[54]
Mixed-grass prairie ‡	GC ₃ , GC ₄ , F	N	CO ₂	[55]
Shortgrass steppe	GC ₄	N, Dig	D	[56]
Shortgrass steppe	GC ₃ , GC ₄	N, WSC, NDF, ADL, Dig	CO ₂	[57]
Shortgrass steppe	GC ₃ , GC ₄	N	CO ₂	[58]
Shortgrass steppe	GC ₄	N, C/N	CO ₂	[59]
Perennial grasses	GC ₃ , F, L	N, NDF, TNC, Dig	CO ₂	[60]
Perennial grassland	F	P	T	[61]
<i>Gentiana straminea</i> , <i>Potentilla anserine</i>	GC ₃ , Cyp	ADF, ADL, Dig	T	[62]
Meadow				
Mediterranean climate				
<i>Dactylis glomerata</i> , <i>Bromus erectus</i> †	GC ₃	N, TNC	CO ₂	[63]

Semiarid grassland species †	GC ₃ , F, L	N, C/N, WSC	CO ₂	[64]
Annual grassland	GC ₃ , F	N, ADL	CO ₂ , T, W	[65]
Annual grassland species	GC ₃ , F	N	CO ₂	[66]
Annual grassland	GC ₃ , F	N	CO ₂	[67]
Grassland and forest trees	F, L, Woody	N, TNC	CO ₂	[68]
Forest and shrubland	Woody	N, C/N	D	[69]
<i>Cynodon dactylon</i>	GC ₄	N, P	W	[70]
Various climates				
US grasslands	GC ₃ , GC ₄	N, Dig	T, D	[71]

† based on information provided by the authors and on Holdridge classification of biomes; † experiment in tunnels; † greenhouse; † growth chambers; G: grasses (C₃ or C₄ photosynthetic types); F: non-N fixing dicots; L: N-fixing dicots; Cyp: *Cyperaceae*; ADF: acid detergent fibre; ADL: acid detergent lignin; NDF: neutral detergent fibre; Dig: digestibility; WSC: water soluble carbohydrates; TNC: total non-structural carbohydrates; CO₂: atmospheric CO₂ enrichment; T: warming; D: rainfall/irrigation reduction; W: irrigation

[1] Dijkstra *et al.* (2008), [2] Dijkstra *et al.* (2010), [3] Dijkstra *et al.* (2012), [4] Evans and Burke (2013), [5] An *et al.* (2005), [6] Lilley *et al.* (2001), [7] Newman *et al.* (2005), [8] Ross *et al.* (2002), [9] Verburg *et al.* (2009), [10] Albert *et al.* (2011), [11] Allard *et al.* (2003), [12] Bertrand *et al.* (2008), [13] Brosi *et al.* (2011), [14] Brown *et al.* (2005), [15] Crous *et al.* (2010), [16] Daepf *et al.* (2000), [17] Daepf *et al.* (2001), [18] Deetz *et al.* (1996), [19] Fischer *et al.* (1997), [20] Frehner *et al.* (1997), [21] Halim *et al.* (1989), [22] Hunt *et al.* (2005), [23] Knops *et al.* (2007), [24] Larsen *et al.* (2011), [25] Newman *et al.* (2003), [26] Newton *et al.* (2010), [27] Piva *et al.* (2013), [28] Read and Morgan (1996), [29] Rodgers *et al.* (2012), [30] Seguin *et al.* (2002), [31] Sheaffer *et al.* (1992), [32] Sheaffer and Seguin (2009), [33] Skinner *et al.* (2004), [34] Soussana *et al.* (2005), [35] Walter *et al.* (2012a), [36] Walter *et al.* (2012b), [37] Zanetti *et al.* (1997), [38] Aerts *et al.* (2009), [39] Gong *et al.* (2011), [40] Hansen *et al.* (2006), [41] Muntifering *et al.* (2006), [42] Sharp *et al.* (2013), [43] Welker *et al.* (2005), [44] Baxter *et al.* (1994), [45] Baxter *et al.* (1995), [46] Benot *et al.* (2013), [47] Cantarel *et al.* (2013), [48] Carrillo *et al.* (2012), [49] Inauen *et al.* (2012), [50] Jensen *et al.* (2003), [51] Jensen *et al.* (2010), [52] King *et al.* (2004), [53] Klein *et al.* 2007, [54] Körner *et al.* (1997), [55] LeCain *et al.* (2012), [56] Milchunas *et al.* (2004), [57] Milchunas *et al.* (2005), [58] Morgan *et al.* (2001), [59] Newingham *et al.* (2013), [60] Picon-Cochard *et al.* (2004), [61] Rui *et al.* (2012), [62] Xu *et al.* (2002), [63] Castells *et al.* (2002), [64] Grunzweig and Körner (2001), [65] Henry *et al.* (2005), [66] Hungate *et al.* (1996), [67] Hungate *et al.* (1997), [68] Körner and Miglietta (1994), [69] Sardans *et al.* (2013), [70] Utrillas *et al.* (1995), [71] Craine *et al.* (2010). The full list of references is available from the authors.

III - General trends

1. Elevated CO₂ effect

Elevated CO₂ decreased by an average of 9% forage nitrogen content and increased by about 30% the non-structural carbohydrates (total, soluble, starch) of forage tissues (Fig. 1a). Also water soluble carbohydrates (WSC) increased, but with very high variability that could result from the instability of soluble carbohydrates within plant tissues (source/sink relationships are affected by elevated CO₂), but also from time of harvest, organs or analytical method. These responses confirm the conclusions of several meta-analyses or reviews (Soussana *et al.*, 2002; Lüscher *et al.*, 2004; Hopkins and Del Prado, 2007; Soussana and Lüscher, 2007; Wang *et al.*, 2012; Xu *et al.*, 2013), but an original output from our meta-analysis is the absence of effect of elevated CO₂ on structural carbohydrates (NDF, ADF, lignin), and digestibility.

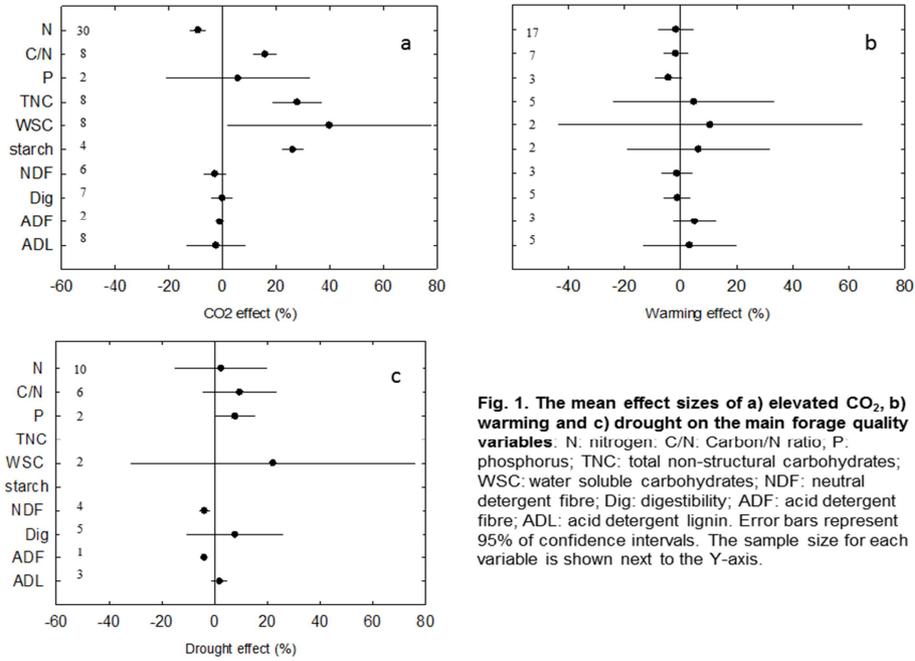


Fig. 1. The mean effect sizes of a) elevated CO₂, b) warming and c) drought on the main forage quality variables. N: nitrogen; C/N: Carbon/N ratio; P: phosphorus; TNC: total non-structural carbohydrates; WSC: water soluble carbohydrates; NDF: neutral detergent fibre; Dig: digestibility; ADF: acid detergent fibre; ADL: acid detergent lignin. Error bars represent 95% of confidence intervals. The sample size for each variable is shown next to the Y-axis.

Effects of elevated CO₂ on digestibility were measured in seven experiments (Table 1; Fig. 1a) but only three (Allard *et al.*, 2003; Picon-Cochard *et al.*, 2004; Milchunas *et al.*, 2005) simultaneously measured nitrogen, and structural and non-structural carbohydrates (average ratios of elevated CO₂ / ambient CO₂ were: non-structural carbohydrates = 1.271; N = 0.929; NDF = 0.985; ADF = 0.984; digestibility = 0.999). The results are thus close to the general trend (Fig.1a). In a shortgrass steppe, Milchunas *et al.* (2005) however reported a decline of digestibility, which is consistent with the slight decrease of non-structural carbohydrate and nitrogen contents while fibre content increased. Differences between experiments could result from variations in species composition (Allard *et al.*, 2003), proportion of tissues with contrasting digestibility, and environmental factors (e.g. soil nutrients). As a consequence of the increase in atmospheric CO₂ concentration, we can hypothesize changes in forage protein-energy balance that are likely to modify microbial synthesis in the rumen and affect digestibility (Soussana *et al.*, 2002). Increase in the non-structural carbohydrate content of forages could be an advantage for fast acidification of forages while making silage, so that no or less additive would be necessary.

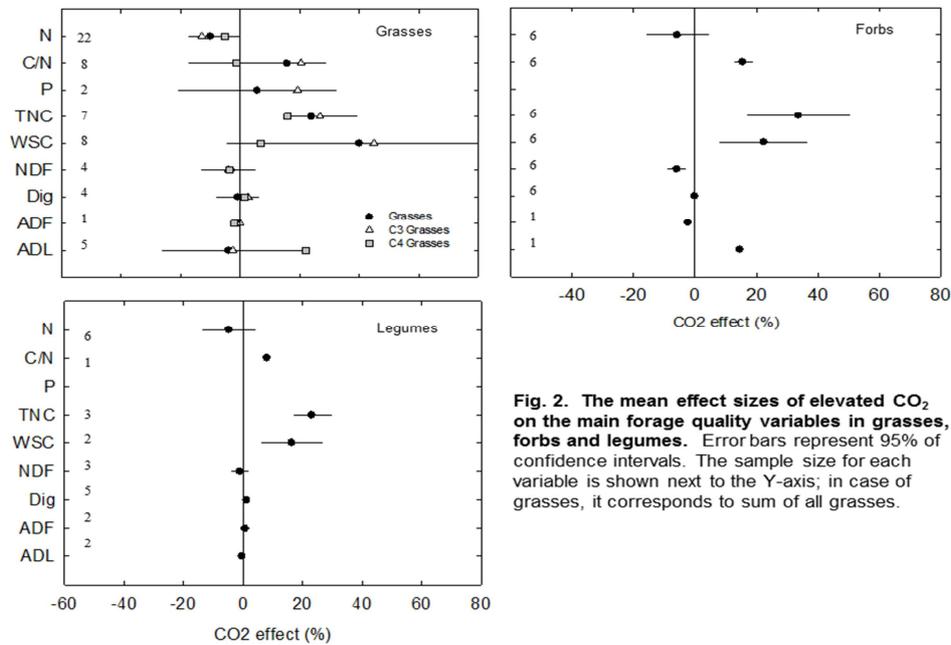


Fig. 2. The mean effect sizes of elevated CO₂ on the main forage quality variables in grasses, forbs and legumes. Error bars represent 95% of confidence intervals. The sample size for each variable is shown next to the Y-axis; in case of grasses, it corresponds to sum of all grasses.

For all quality variables, we observed the same response between functional groups (Fig. 2). Within grasses, only N and C/N ratio responded slightly differently between C₃ and C₄ grasses, with a lower N ratio for C₃ (-13%) than for C₄ (-5%), and thus a higher C/N ratio for C₃ grasses. This is consistent with the conclusions of Wang *et al.* (2012) who compared C₃ and C₄ species response, including woody species and crops, to elevated CO₂. This more neutral effect of elevated CO₂ on the N content of C₄ grasses, results from the photosynthesis and biomass accumulation of C₄ species being less affected by elevated CO₂ than those of C₃ species.

Shifts in species composition in response to elevated CO₂ could however strongly impact overall forage digestibility in grazed pastures (Morgan *et al.*, 2004; Milchunas *et al.*, 2005). The considerably lower concentration of N under elevated CO₂, observed for *Lolium perenne* leaves in pure stands of the Swiss FACE experiment, was found to a much lesser extent for *L. perenne* grown in mixture with *Trifolium repens* (Zanetti *et al.*, 1997; Hartwig *et al.*, 2000). Highly important, in the mixture the proportion of N-rich *T. repens* increased at the expense of the N-poorer *L. perenne* from 21% at ambient CO₂ to 33% at elevated CO₂ (Hebeisen *et al.*, 1997; Daepf, 2000). In more complex mixtures containing other grasses, legumes and non-leguminous dicot species, the proportion of legumes in the community also increased significantly under elevated CO₂ (Lüscher *et al.*, 1996; Campbell *et al.*, 2000), especially when the community was frequently cut (Teyssonneyre *et al.*, 2002). As a result, the concentration of N in the harvested biomass of the mixture showed no significant reduction under elevated CO₂ (Lüscher *et al.*, 2004). These results demonstrate that the response of plant communities cannot be predicted from the response of individual species grown in pure swards, and that CO₂ induced changes in the proportion of species with differing forage quality may be more important than CO₂ induced changes in the quality of individual species.

2. Warming effect

The meta-analysis did not reveal any significant effects of warming on N, NDF, ADF, WSC and digestibility (Fig.1b). Similar patterns were found for grasses, forbs and legumes although few data were available for forbs, legumes (Fig.3) and C₄ grasses. This contrasts with results from two meta-analyses (Dieleman *et al.*, 2012; Bai *et al.*, 2013) and a survey on *Medicago sativa* (Walgenbach *et al.*, 1981) concluding that warming slightly increased plant N content. Higher

mineralization in warmer soils can indeed increase soil N availability and consequently plant N uptake. However, reduced soil moisture can also cause highly stressful conditions that are likely to mitigate the effects of an increase in soil N availability on plant uptake; this could explain contrasting trends in the effect of warming on forage N content.

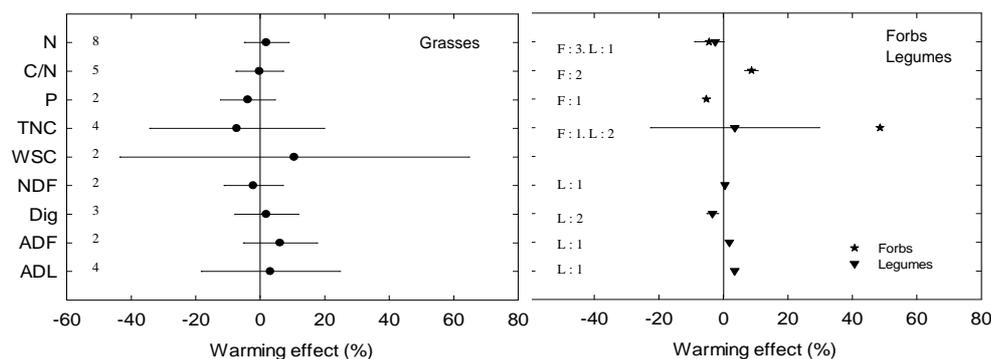


Fig. 3. The mean effect sizes of warming on the main forage quality variables in grasses, forbs and legumes. Error bars represent 95% of confidence interval. Sample size for each variable is shown next to the Y-axis.

According to Buxton and Fales (1994) temperature is the main factor that influences the nutritive value of forages. In general, a rise in temperature increases plant growth, reduces leaf:stem ratios and increases NDF, ADF and lignin contents. Consequently, digestibility is usually reduced. When changes in temperature occurred over the growing season, the effects of temperature, ontogeny and maturity are confounded. In our meta-analysis, we compared the chemical composition of the same organs or plants under ambient or elevated temperature. The effect of warming has been shown to modify fibres and digestibility differently in leaves and stems (Wilson *et al.*, 1991). Here, the absence of clear effects of warming on plant chemical composition and digestibility could result from the fact that measurements carried out on different organs were mixed in the meta-analysis. It also suggests that the effects of warming on forage quality could mostly be driven by the evolution of plant phenology.

Indirect effects of warming could also arise from shifts in sward botanical composition. The amplitude of these indirect effects is assumed to vary according to climatic conditions and plant communities (Izaurrealde *et al.*, 2011; Rodgers *et al.*, 2012). Simulations in the Aubrac area of Central France predicted a shift towards exploitative grasses of higher digestibility as the result of a 1.2°C warming (Picon-Cochard *et al.*, 2013). Cantarel *et al.* (2013) observed that an average 3.5°C warming during 4 years decreased grass proportion by 10% at the expense of legumes (mainly *Vicia* sp.), increasing forage N content in this upland permanent grassland.

3. Drought effect

Overall, experiments investigating the effect of drought on forage quality are rarer than those manipulating atmospheric CO₂ or temperature. In the meta-analysis, ten studies analyzed the effects of drought on forage nitrogen concentration (six for C/N) with never more than five experiments for other parameters (Fig. 1c). Drought led to an average 5% decrease in plant cell-wall (NDF) content. Digestibility increased on average by 10%, with strong variations between experiments (Halim *et al.*, 1989; Deetz *et al.*, 1996; Skinner *et al.*, 2004; Milchunas *et al.*, 2004; Craine *et al.*, 2010). The lack of clear drought effect could be the consequence of the small amplitude of NDF variations, a small increase in lignin content sometimes counteracting the decrease of NDF. We highlighted a continuum in the effect of variations in precipitation from reduction (drought) to irrigation on plant N response, i.e. the ratio of N content between drought (or irrigation) and control values, with a curvilinear increase of forage N response as water

availability decreased (Fig. 4). Variability of N and C/N forage contents was greater compared with experiments in which atmospheric CO₂ or temperature were manipulated (Fig. 1). Yet data from the literature on the effect of periods of low precipitation on plant N concentration are conflicting, with some authors reporting a reduction (Hayes, 1985; Craine *et al.*, 2010) and others an increase (Murphy *et al.*, 2002). A reason for this could be the shifts in community structure that were observed as a response of grassland ecosystems to drought. Increases in dominant perennial forbs and decreases in dominant grasses have for instance been reported with warming and summer drought in the UK (Sternberg *et al.*, 1999). Legumes, such as white clover, decreased under drought conditions while other species such as the deep-rooted chicory tended to yield well (Skinner *et al.*, 2004). Variations in forage N content can thus be expected since legumes are richer in N than other functional groups. Some legumes such as sainfoin or alfalfa are known to be drought tolerant and their persistence could maintain or even increase forage N content. Finally, it is noteworthy that legume quality can increase under drought conditions due to a higher leaf-to-stem ratio, delayed maturity, and higher quality of both the leaf and stem fractions (Peterson *et al.*, 1992).

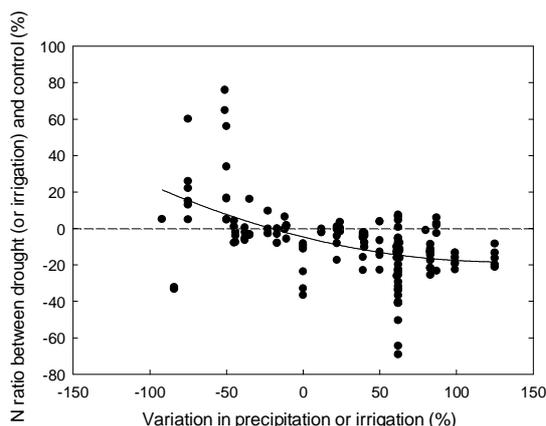


Fig. 4. Effect of variations in precipitation from reduction (drought, i.e. negative values on the X-axis) to irrigation (positive values) on plant N response, i.e. the ratio of N forage content between drought (or irrigation) and control. Values at 0 on the X-axis are drought experiments in which average precipitation was kept constant but increased in variability (Walter *et al.*, 2012a,b).

IV - Specificities of mountain and Mediterranean areas - further research needs

1. Mountain areas

The meta-analysis allowed us comparing the outputs from 19 climate manipulation experiments under mountain climate conditions, with those from 28 papers from temperate plains (Table 1). Mountain was defined based on the altitude that was above 800 meters. Within temperate plains, we considered lowland sites under either oceanic or continental influence, with mean annual temperature above 6°C separating the latter from sub-arctic climate in Holdridge classification. Applying some particular climate change factors in a controlled way and analyzing their direct effects on forage quality did not allow identifying specific trends for the effects of elevated atmospheric CO₂ in mountain areas (Fig. 5). Overall, N concentration was reduced by 10% ($\pm 5\%$) vs 11% ($\pm 4\%$) in temperate plains. Water soluble carbohydrates were increased by 54% in mountain areas (vs 27% for temperate plain) but with huge experimental variations that

prevent concluding on any significant difference. Only Picon-Cochard *et al.* (2004) and Milchunas *et al.* (2005) analyzed the effect of elevated CO₂ on the NDF content of upland swards; it was on average similar to that in current CO₂ conditions (Fig. 5b). A recent experiment revealed a slight but significant 3% decrease in NDF herbage content as the result of elevated CO₂ (+ 140 ppm), while N forage content decreased by 13%; consistently digestibility remained unchanged (Niderkorn *et al.*, 2014). Perhaps more significant are the theorized shifts in vegetation composition predicted in future CO₂-enriched environments, with some evidence in mountain areas (Teyssonneyre *et al.*, 2002; Stampfli and Zeiter, 2004). Rising atmospheric CO₂ concentration has the potential to cause significant alterations in grassland structure and function, with some outcomes leading to grasslands that are more productive but of lower forage quality for domestic livestock (Campbell *et al.*, 2000).

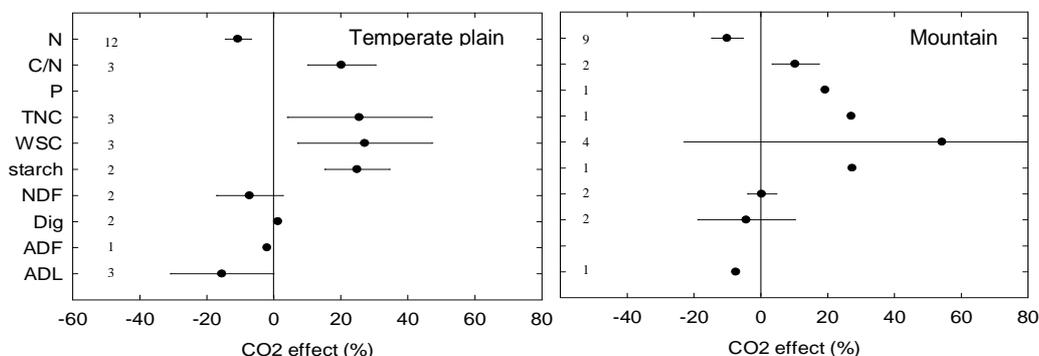


Fig. 5. The mean effect sizes of elevated CO₂ on the main forage quality variables in mountains (> 800m a.s.l.) and temperate plains (oceanic or continental with annual temperature > 6°C). Error bars represent 95% of confidence intervals. The sample size for each variable is shown next to the Y-axis.

The effects of increasing average air temperature (six experiments) or reducing precipitations (three experiments) were even less analyzed in mountain areas. We identified some contrasting trends on the direct effects of increasing air temperature since forage N content increased by an average of 9% ($\pm 7\%$) under mountain climate conditions compared with a 2% decrease ($\pm 9\%$) in temperate plains. This increase in forage N concentration in mountain areas is consistent with the results from two meta-analyses (Dieleman *et al.*, 2012; Bai *et al.*, 2013). According to what we discussed in section 3, it suggests non-limiting soil water conditions in most mountains areas (at least in those where climate manipulation experiments have been conducted so far). Consistently, productivity in subalpine grasslands in the Pyrenees was reported to be more temperature-limited than water-limited (Sebastià, 2007). Shifts in plant community structure as the result of warming could have further positive effects on forage quality, e.g. the increase of legume abundance in perennial grasslands in the French Massif-Central (Cantarel *et al.*, 2013), or of exploitative grasses in the Aubrac region (Picon-Cochard *et al.*, 2013). Effects of an extreme summer event (i.e. a 2-week heat wave at +6°C combined with a 3-month summer drought) differed from those of moderate warming (+2°C). Niderkorn *et al.* (2014) found that both sward biomass and quality dropped during the extreme event, but in the autumn the N content of re-growing tissues increased by 35% while NDF decreased by 7%; this led to a significant 8% increase of forage *in vitro* digestibility, which contrasts with what is reported in Figure 5b.

Only three experiments investigated the effect of reducing water availability on forage quality in mountain grasslands. Consistent with the general trend reported in Figure 4, the N content of forages increased with water shortage whether it was applied alone or in combination with other factors (Milchunas *et al.*, 2004; Benot *et al.*, 2013; Cantarel *et al.*, 2013). Water soluble carbohydrates increased in subalpine grasslands as the consequence of an increase in air

temperature and of summer drought (Benot *et al.*, 2013). In vitro digestibility of forages also increased in a shortgrass steppe as the result of water shortage (Milchunas *et al.*, 2004).

More generally, warming and changes in water availability can modify the boundaries of productivity defined seasons and seasonal herbage surplus or shortage. A positive effect of warming in mountain areas would be the decrease in the length of the winter period. Shorter winters reduce animal feed stock needs and allow an earlier start of sward growth which may allow a more intensive exploitation (additional cuts or mowing at higher altitude) of resources when spring and summer droughts are not too severe (Nettier *et al.*, 2010). A high year-to-year variability in temperature and rainfall could however threaten the capability of high-altitude grasslands to provide high quality forages during summer. In the Pyrenees, shifts in botanical composition could have negative effects on forage quality since some highly palatable grasses, such as *Festuca nigrescens*, were negatively affected by climate change, while less palatable forbs (e.g. *Potentilla neumanniana*, *Euphorbia cyparissias*) became abundant (Sebastià, 2007). Interactions between climate and management could be relevant in this context. Both grazing and changes in cutting regimes (e.g. early cuts) could buffer the negative effects of climate change on forage quality, so that it is likely that pasture management offers promising options for adapting livestock systems to climate change.

2. Mediterranean areas

The meta-analysis led us to analyze the data from only eight experiments, the effect of elevated CO₂ being the most frequently tested (Table 1). Nitrogen concentration was recorded in all the experiments. On average, forage N content was only reduced by 1% (\pm 9%) vs -11% (\pm 4%) for temperate plains. This could either result from shifts in vegetation communities or from a concentration of N in plant tissues under drought conditions (Fig. 4). Both WSC and TNC increased as the result of elevated CO₂, which is consistent with overall trends reported in Figure 1a. No measurement of digestibility was made in any of these climate manipulation experiments. In Mediterranean areas, the increment of plant biological activity can be slowed down by soil water scarcity, but due to the lack of data we mainly base our discussion on measurements of the quality of forages adapted to Mediterranean areas.

Mediterranean grasslands quality is often limited by the lack of legumes. P-fertilization and liming on native pastures are effective methods to increase legumes in grasslands thus promoting N fixation (Cocks and Gintzburger, 1993). Annual self-reseeding legumes (e.g., subclover and medics) have been extensively used for pasture improvement in the Mediterranean basin for over forty years; in resources-poor drylands, they represent a valuable source of protein that mitigates the negative effects of drought and warming of forage production (Porqueddu, 2001). Possibilities to exploit the genetic resources of perennial legumes that are able to escape summer drought and regrow at the season break e.g. *Sulla coronaria*, *Onobrychis viciifolia* (Sulas, 2005; Re *et al.*, 2014) offer opportunities to stabilize both production and forage quality. Several breeding programs, especially in Australia and New-Zealand, focused on the production of deep-rooted and drought tolerant perennial legumes (e.g., Caucasian clover, stoloniferous red clover, tallish clover, etc.), which have a high feeding value that declines slowly with maturity. Recent research indicates that *Psoralea bituminosa* L. Stirton also has potential as a highly-nutritive forage legume for Mediterranean disadvantaged areas (Reaside *et al.*, 2013).

In perennial grasses, some Mediterranean varieties of tall fescue, cocksfoot and phalaris are adapted for climate with annual rainfall >500 mm and accumulated summer water deficit <700 mm (Lelièvre *et al.*, 2008). Summer dormancy and dehydration tolerance are considered as the main drought tolerance traits (Norton and Volaire, 2012). Porqueddu and Carneiro (unpubl. data) conducted a multi-site comparison that revealed the higher digestibility of seven cocksfoot cultivars (except for subsp. *hispanica* Kasbah) compared with six tall fescue cultivars. Wide intra-specific variability was observed for N, NDF, ADF and ADL content, and digestibility. This experiment showed that most perennial grass varieties that are able to persist over long summer drought combine early autumn regrowth with high crude protein content (e.g., 23.5%

for the Sardinian ecotype Ottava). In winter and spring, crude protein content is halved and fibre content generally decreases, which tends to buffer digestibility. Little work has been done on the selection of reed canarygrass and perennial ryegrass. According to Gutman *et al.* (2001), more information on the effects of defoliation and grazing on biomass partitioning in perennial grasses is needed to improve the forage quality and production efficiency in Mediterranean grasslands.

Pasture mixtures available in southern Europe consist in a small number of annual legumes (subclover, medics, etc.) sometimes including low proportions of annual grasses (e.g. annual ryegrass, Italian ryegrass). In areas with higher rainfall, perennial grasses, such as cocksfoot and reed canarygrass, are used in mixtures. It is also frequent to find complex mixtures including up to 15-20 species (Porqueddu and Gonzales, 2006). Compared with pure stands, grass-legume mixtures provide higher yields with better seasonal distribution and limit the spreading of unsown species. The feeding value of the different grass-legume mixtures has been discussed by Maltoni *et al.* (2007). Mixtures have less seasonal variations in quality compared with pure stands. According to Norton and Volaire (2012), it may thus be possible to develop a stable pasture mixture comprising summer dormant and summer active species/varieties so that any moisture available throughout the year can be utilized by one of the mixture component. Our meta-analysis did not reveal any variations in the response of grasses, forbs and legumes to elevated CO₂, warming and drought. Climate change is thus not expected to directly affect the chemical composition of grasses and legumes, but could shift their relative abundance in mixtures according to the previously discussed adaptations of functional types.

V - Conclusion

In this review, we analyzed the single effects of elevated CO₂, warming or precipitation change on the main forage characteristics. While many studies have investigated changes in nitrogen content, less information is available for non-structural carbohydrates. Fibres and *in vitro* digestibility were recorded in a very limited number of studies, and were on average similar to those in current climatic conditions. Overall, we thus did not observe any dramatic change in forage quality induced by climate change factors, apart from those that may result from shifts in grassland botanical composition. The combined effects of climate change factors and the effect of extreme events were seldom investigated. Our meta-analysis outputs (e.g. contrasting response of N to each factor in Figure 1), literature reviews (Dieleman *et al.*, 2012) and some pioneer experiments testing combinations of climatic factors (Read and Morgan, 1996; Larsen *et al.*, 2011; Cantarel *et al.*, 2013) suggest that their combined effects on forage quality cannot be easily predicted from single factor responses. Further experiments should thus be carried out focusing on these combined effects. In addition, response to extreme events can differ from those obtained under moderate warming and drought (Benot *et al.*, 2013; Niderkorn *et al.*, 2014), and should thus be further tested. Very few data are also available for Mediterranean areas, which prevented any comparison apart from the response of N forage content to elevated CO₂. The field manipulation experiments we used in the meta-analysis have a strong predictive power, and allow a precise monitoring of all system variables. However, they may exacerbate the effects of natural climatic changes on plant ecosystem processes (Leuzinger *et al.*, 2011), which might in turn affect forage quality. Management options could buffer the effects of climate change on forage quality. However, they were only investigated in a limited number of studies with mown grasslands (e.g. Zanetti *et al.*, 1997; Daepf *et al.* 2000; Picon-Cochard *et al.*, 2004). Long-term experiments that follow vegetation dynamics as a response to climate variability (LTER in the US, SOERE in France, etc.) are closer to natural pedoclimatic conditions, take account of climate variability (gradual natural trends, extreme events), and allow testing for the effects of grazing management. It is thus likely that predicting forage quality from grasslands in a changing climate will require both approaches to be pursued in a coordinated way.

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